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University of Alaska PH.D. 1982

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A

THESIS

Presented to the Faculty of the University of Alaska

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

by

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Fairbanks, Alaska

May, 1982

NITROGEN DYNAMICS THROUGH THE FOREST FLOOR

OF TWO INTERIOR ALASKA BLACK SPRUCE ECOSYSTEMS

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April 16, 1982.

Date

ABSTRACT

Nitrogen flow in the forest floor of two interior Alaska black spruce (Picea mariana (Mill.) B.S.P.) ecosystems was investigated and related to environmental constraints unique to the area, specifically temperature, moisture, and organic matter quality (C/N ratio). Pools examined were NH_4-N, NO_3-N, soluble organic N, total (Kjeldahl) and residual organic N. Low addition levels of high enrichment isotope (<1% of the total nitrogen pool with 99 atom percent excess ^{15}N) were used to describe nitrogen dynamics through pools of selected forest floor components of permafrost-free and permafrost-dominated black spruce sites.

A thick carpet of mosses, made up primarily of the feather moss species Hylocomium splendens (Hedw.) B.S.G. and Pleurozium schreberi (B.S.G.) Mitt. played a vital role in the nitrogen economy of the forest floor. Nitrogen, quickly immobilized in the moss layers (green, brown) and retained there, was released very slowly and sequestered in the fermentation and humus layers (021+022) where most of the vascular plant roots were located. Vascular understory ^{15}N uptake was minimal as was ^{15}N export via the soil solution.

Periodic mineralization episodes, more frequent and dynamic at the permafrost-free site (where C/N ratios were lower), were largely restricted to the moss layers since available N pools in deeper forest floor layers incorporated little label over the three year period.

It proved difficult to separate the effects of rainfall events from that of forest floor temperature fluctuations upon seasonal nitrogen dynamics. In the lower layers of the forest floor temperature and/or moisture rather than organic matter quality appeared to be the overriding factor controlling N flow.

The dominance in pool size of NH_4-N over NO_3-N is discussed with reference to current theories of ecosystem strategy.

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ACKNOWLEDGEMENTS

One of the pleasures of submitting this thesis is the opportunity to have a forum for thanking my supervisor, Dr. Keith Van Cleve. He was always generous with his time and expertise and gave freely of his wisdom and professionalism. The kindness and friendship he extended to my family and myself will always be remembered and cherished.

I was fortunate in assembling my supervisory committee, represented by Drs. Vera Alexander, F. S. Chapin, III, J. F. Fox and L. A. Viereck. They always fitted me into their busy schedules when I needed help and this is gratefully acknowledged. Special thanks should go to Dr. Vera Alexander for providing access to the mass spectrometer at the Institute of Marine Science and to Dr. L. A. Viereck, who, during our site visits along the Tanana River, shared his experience and understanding of more circumpolar ecosystems than I will ever know.

I would like to thank Messr. R. E. Schlentner and D. M. Hoch from the Forest Soils Laboratory and Institute of Northern Forestry, respectively, for weather data collection on the two black spruce sites. They efficiently reduced the data and quickly made them available to other people.

Dr. C. T. Dyrness from the Institute of Northern Forestry provided the soil profile description at Bonanza Creek. Going to the field with the Forestry people invariably made a field day more

interesting and enjoyable than it usually was.

I thank Dr. R. White from the Institute of Arctic Biology for participating in several very useful discussions dealing with the problems of tracer kinetics.

Ms. L. K. Oliver, Laboratory supervisor at the Forest Soils Laboratory, kept things running smoothly at all times and made all of our jobs easier, often through no help of ours.

I am grateful to Mr. R. J. Candler for initiating me into some of the more obscure aspects of organic chemistry when the need arose and to Mr. C. E. Johnson for demonstrating what the proper technique for chemical analyses is really all about.

I am indebted to the United States for making my stay in Alaska a fruitful one and in particular for providing financial assistance through a grant to the University of Alaska from the McIntire Stennis Cooperative Forestry Research Program.

Finally, I have to thank my wife Wally who cheerfully braved not only the climate, but also my occasional episodes of anticipatory impending doom triggered by such events as comprehensive exams or the writing, revisions and defense of this thesis.

INTRODUCTION

Rationale

Black spruce (*Picea mariana* (Mill.)B.S.P.)[a] is one of the most abundant conifers of northern North America. Its range extends from Newfoundland and the northeastern United States west and northwest to northwestern Alaska. It grows south to central British Columbia, southern Manitoba, central Minnesota, southeastern Michigan, and Pennsylvania. Although most of the range is in Canada, there are important stands of this spruce in the Lake States, notably in Minnesota and Upper Michigan (Fowells, 1965). In interior Alaska, occupying areas of continuous as well as discontinuous permafrost (Viereck and Little, 1975), it is recognized as the most widespread forest type and also the type with the highest frequency of fire (Viereck *et al.*, 1979). Black spruce forests, with a minor component of tamarack (*Larix laricina* (Du Roi) K. Koch), take up 33.5 million ha or 78% of the total forested area in interior Alaska (Hutchison, (1967). In terms of commercial exploitation of timber resources, interior Alaskan black spruce forests compare unfavorably with stands located in more temperate regions of its range. For example, Barney and Van Cleve (1973) working in interior Alaska, estimated above ground whole tree biomass as 16×10^3 kg/ha and 24×10^3 kg/ha for 50 year old lowland and upland black spruce stands respectively. In contrast,

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[a]Vascular flora nomenclature follows Hultén (1968).

the same tree components in eastern Canadian black spruce stands of comparable age were assessed as 196×10^3 kg/ha and 107×10^3 kg/ha in Ontario (Gordon, 1979) and Quebec (Weetman and Webber, 1972), respectively. Although interior Alaskan black spruce forests are not presently considered commercially productive for timber, they are of considerable value for watershed protection and wildlife habitat (Lutz, 1956; Troth et al., 1976). Therefore, some basic understanding has to be gained regarding the ecological controls that are acting on these ecosystems, if land use managers are to make informed decisions regarding these vast tracts of land.

The Forest Floor

One of the most important components and an integral part of any forest ecosystem is the forest floor with its organic layers. The importance of the forest floor, not only in terms of the mass it contributes to the overall ecosystem, but also as a major reservoir of organic matter and nutrients and its regulatory role in most of the functional processes occurring throughout the ecosystem is now well recognized (Bormann and Likens, 1979; Gosz et al., 1976).

The physical and chemical characteristics of the forest floor are a natural function of such factors as climate, vegetation, time, and topography (Jenny, 1980; Olson, 1963). Organic matter accumulation under mature forests may exceed the living biomass (Rodin and Bazilevich, 1967) and this is certainly true for black spruce ecosystems in interior Alaska. According to Barney and Van Cleve (1973)

the forest floor weight exceeds that of the standing live overstory tree material by a factor of at least four. In more temperate parts of the range of black spruce, mature forest floor weight may be only slightly higher than tree biomass (Weetman and Webber, 1972) or lower (Gordon, 1979), reflecting either climatically more favorable conditions for decomposition processes (Rodin and Bazilevich, 1967), improved organic matter quality (reduced decay resistance), more rapid tree growth rate or a combination of these factors.

In interior Alaska, black spruce stands are typically restricted to the poorest quality sites, such as poorly drained, permafrost bottomland or north-facing slopes which receive reduced solar radiation. The controlling factors leading to the formation of the thick forest floor in these stands are not thoroughly understood, but several lines of evidence suggest that changes in plant cover effect changes in soil temperature. At some point in the development of the black spruce stand, regardless of origin or site, a thick and continuous moss layer develops providing effective thermal insulation for the underlying organic layers (Van Cleve et al., 1980; Viereck, 1970a; 1970b). During the summer the upper layers of the moss/organic matter complex become dry through evaporation. Under such conditions the thermal conductivity of this medium is low, hence warming of lower layers is impeded. The lower forest floor horizons gradually thaw downward and become wet in response to melting of seasonally frozen layers. Following autumn rains there tends to be more

moisture in the surface layers of the forest floor in response to lower evaporation rates due to lower ambient temperatures. When the forest floor freezes at the onset of winter its thermal conductivity is increased considerably. Thus, less resistance is offered to cooling of the forest floor in winter than to warming of it in the summer (Brown, 1973; Viereck, 1970a). The thick moss mat, therefore, seems to be primarily responsible for setting off this negative feedback loop, whereby thawing becomes progressively slower in the soil, resulting ultimately in permafrost formation. The frozen soil prevents water percolation and the resulting wetter and colder soils inhibit tree growth while favoring further moss development (Viereck, 1970a).

Low soil temperature has been shown to be the major factor inhibiting decomposition in subarctic spruce-lichen woodland soils with acidity, low N content, lack of readily available carbon, and low mesofaunal populations of secondary importance (Moore, 1981). Thus, decreased decomposition rates can be expected to be conducive to further organic matter accumulation and increase in forest floor thickness. If the moss and organic layers have developed sufficiently, the mineral layer may be entirely frozen and all tree roots become located in the forest floor organic layers. Nutrients in the organic layer are depleted, and some elements such as phosphorus, nitrogen, and manganese may become limiting (Viereck, 1970b). Therefore, the forest vegetation exists on a progressively more deficient substrate and the forest floor increasingly acts as a sink for

ecosystem nutrient capital.

Figure 1 shows pool sizes and annual incorporation of organic matter as well as nitrogen in compartments of a permafrost-free black spruce ecosystem in interior Alaska. The forest floor is clearly the dominant compartment with respect to organic matter and nitrogen content in view of the fact that root exploration is largely restricted to this layer. The importance of the mosses, which are in intimate contact with the forest floor, is emphasized by their proportionately large annual uptake rates.

The Mosses

The principal moss species on the black spruce forest floor in this study are Pleurozium schreberi (B.S.G.)Mitt. and Hylocomium splendens (Hedw.) B.S.G.[b] Their widespread association with black spruce in circumpolar lands has been documented by Weetman and Timmer (1967) for eastern Canada, Horton et al. (1979) and Busby et al. (1978) for Alberta, and Tamm (1953) for Scandinavian spruce forests.

Most studies dealing with these feather mosses have focused on their photosynthetic activities, growth and reproduction (Bates, 1979; Busby et al., 1978; Callaghan, et al., 1978; Longton and Greene, 1979) and the accumulation of heavy metals from smelter operations (Barclay-Estrup and Rinne, 1978; Rinne and Barclay-Estrup, 1980; Ruhling and Tyler, 1970). Only a few studies attempted to integrate the functional characteristics of the moss mat with those of the underlying forest

[b] Nonvascular flora nomenclature follows Cunningham (1972).

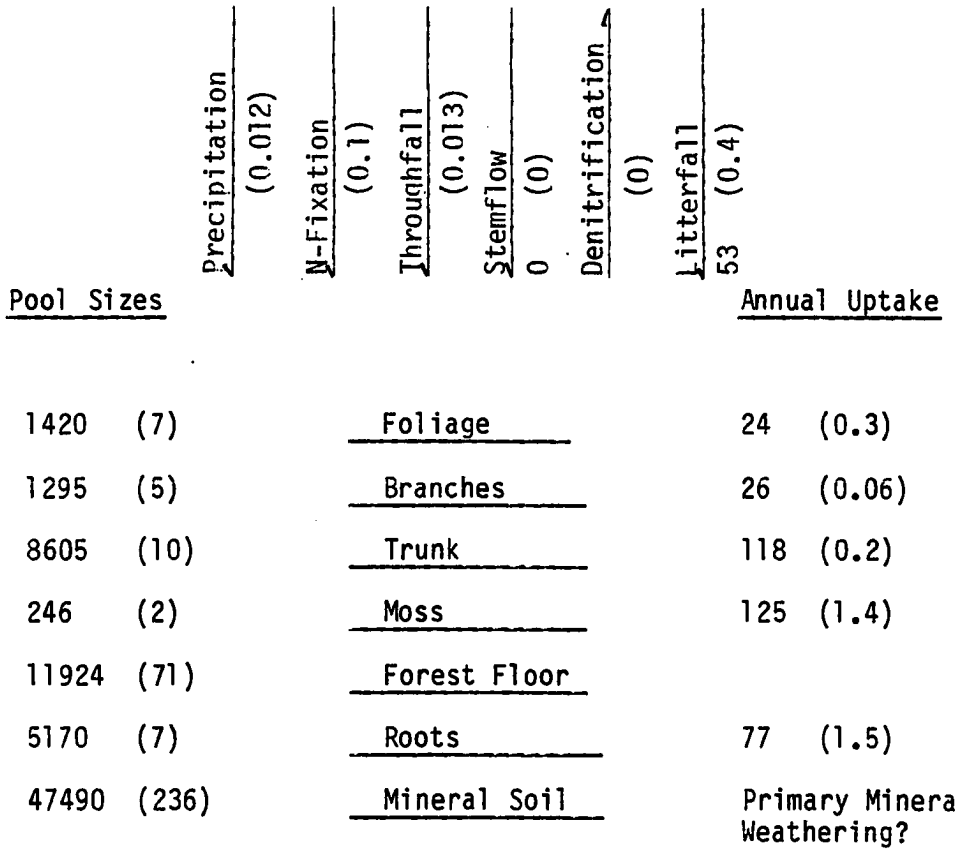

Figure 1. Organic matter and nitrogen pool sizes and annual uptake in a 130 year old permafrost-free black spruce ecosystem in interior Alaska. Units in $g \cdot m^{-2}$. Nitrogen in parentheses (modified from Van Cleve *et al.*, 1979).

floor and relate them to the ecosystem as a whole. Tamm (1953) considered the moss mat nutritionally independent of the underlying organic layers and mineral soil. He rejected the old [sic] view that Hylocomium splendens and similar mosses obtain their nutrients and water from below. Not only because of the absence of rhizoids and a water conducting system in these plants, but also since experimental results showed that nutrients were to a large extent supplied through leachable salts in the tree crowns, dust and atmospheric ammonia and some nitrate contained in rain. It was suspected that there also may have been direct absorption of ammonia by the plants from the air. These findings were essentially confirmed in later papers by Tamm (1964), Rinne and Barclay-Estrup (1980) and Callaghan et al., (1978), although upward capillary movement of water and ions contained therein along the outside of the plant from below the moss canopy were not considered (Anderson and Bourdeau, 1955; Bellamy and Rieley, 1967; Mägdefrau, 1969). Weetman and Timmer (1967) similarly reported, that feather mosses, quite apart from competing with the trees for nitrogen, may actually be the major source of nitrogen in eastern Canadian black spruce forests, since feather mosses were shown to be associated with nitrogen mineralization during decomposition. These workers concluded that the moss mat represented a rapid means of entry of nitrogen contained in rainfall into the nitrogen cycle of the stand. However, if annual nutrient accumulation by mosses exceeds uptake by trees, the moss layer may represent an effective

bottleneck in the nitrogen cycle of the stand through slow release of available nutrients. Since available forms of nitrogen are considered limiting to plant production in black spruce stands throughout its range (Weetman et al., 1972; Van Cleve and Alexander, 1981), nutrient sequestering by the moss layer would be consistent with modern theories of ecosystem strategy, whereby the system will conserve potentially limiting materials by concentrating them and withholding them from dilution and loss (Callaghan, 1980; Shaver, 1981; Welsh, 1980). This condition may exist in arctic and subarctic ecosystems, where low soil and air temperatures are among the key factors controlling low levels of plant production (Bliss et al., 1973).

The moss layer in subarctic black spruce ecosystems plays another important role related to the nitrogen economy of the stand which is connected to nitrogen additions through nitrogen fixation. Billington (1981) and Billington and Alexander (1978) have shown for interior Alaskan black spruce stands that nitrogen-fixing blue-green algae grow epiphytically in the green feather moss canopy. Their study showed that, although nitrogenase activity (acetylene reduction) was significantly higher in the lichens than in other plant types, there was enough activity exhibited by the moss-algae complex to make it the larger fixing entity based on plant cover. The nitrogen fixing organism was tentatively identified as Nostoc sp. In coniferous forests of subarctic Scandinavia Nostoc sp. has been shown conclusively to be associated epiphytically as well an endophytically with

Sphagnum sp. and fix nitrogen in this association (Basilier, 1979; 1980; Granhall and Lindberg, 1978). Estimated mean annual nitrogen fixation in these Scandinavian coniferous forests amounted to 0.32 g $N \cdot m^{-2} \cdot yr^{-1}$ (Granhall and Lindberg, 1978).

In northern latitudes, low numbers and reduced activity of free-living nitrogen-fixing soil microorganisms, in conjunction with a paucity of legumes and non-leguminous actinorhizal nitrogen-fixing species accentuates the importance of non-vascular plants in nitrogen fixation. Since biological processes associated with soil nitrogen transformations will be reduced in cold-dominated northern ecosystems (Van Cleve and Alexander, 1981), the moss layer and the underlying organic layers assume added importance, for this ecosystem compartment is located in the warmest (and earliest to thaw) portion of the soil profile (Heilman, 1966), experiencing the most drastic seasonal climatic fluctuations.

Isotopic Tracing

The regulatory role of the forest floor and moss layer over nitrogen cycling in northern boreal forest ecosystems can be documented by experimentally blocking various processes involved in element turnover (Vitousek, 1977). For example, the trenched plot and buried polyethylene bag techniques are used to provide information regarding mineralization and nitrification in the absence of either plant uptake or leaching. A more direct and less destructive method involves the use of an isotope of a given nutrient, in the case of this study, ^{15}N.

^{15}Nitrogen is a stable isotope and its usefulness as a longterm tracer in biological systems is based on the fact that ^{14}N and ^{15}N occur naturally in an almost constant ratio. This ratio is about 272:1 i.e., naturally occurring nitrogen contains about 0.366 atom% ^{15}N or about 3660 ppm ^{15}N (Hauck and Bremner, 1976).

Addition of a material enriched with ^{15}N to a system will result in an increase in ^{15}N concentration in all or part of the system, the extent of change depending on how much tracer was incorporated into the various nitrogenous components of the system. The change in nitrogen isotope ratio in samples obtained from the system permits study of the transformations of the added tracer material. The amount of change in isotope ratio from the background level (atom% excess ^{15}N) permits calculation of the extent to which the tracer has interacted with and become part of the system (Hauck and Bremner, 1976).

There are three fundamental assumptions that are central to the use of ^{15}N as a tracer in biological systems: (1) the relative abundance of N isotopes in naturally occurring materials does not vary; (2) the behavior of ^{15}N in physical, chemical and biological processes is identical to that of ^{14}N, hence living systems cannot distinguish one isotope from another of the same element; (3) the chemical identity of isotopes is maintained in biochemical systems (Edwards, 1978; Hauck, 1973; Hauck and Bremner, 1976).

None of these assumptions are entirely valid for all experimental situations (Bremner, 1965; Blackmer and Bremner, 1977), but, as far as

can be ascertained from the literature, their validity has been tacitly assumed for nitrogen tracing studies in terrestrial ecosystems.

The use of ^{15}N to describe nitrogen transformations in quantitative terms is neither simple, easy nor cheap (Broadbent, 1981). Nevertheless, more than 1500 papers relating to the use of ^{15}N tracer techniques have been published since 1943 in agronomy and related sciences alone (Hauck and Bremner, 1976). Nitrogen cycles have been studied with ^{15}N in such diverse habitats as New Zealand pastures (Keeney and MacGregor, 1978), Australian eucalypt forest (Jones and Richards, 1977; 1978), North American grasslands (Clark, et al., 1978) and subarctic boreal forest (Van Cleve and White, 1980). Specific aspects of the nitrogen cycle, such as denitrification, clay fixation of ammonia, nitrogen immobilization and decomposition of organic nitrogen were also studied using ^{15}N (Kowalenko, 1980; Ladd et al., 1981; Rolston and Marino, 1976). Nitrogen fixation (symbiotic) has received a great amount of attention, not only in agricultural systems (Ohyama and Kumazawa, 1979), but also (non-symbiotic) in natural ecosystems, such as subtropic and temperate coniferous forests (Bevege et al., 1978; Jones, 1978), northern boreal forest (Basilier, 1980) and arctic tundra (Alexander and Schell, 1973).

Forest floor nitrogen cycling studies using ^{15}N were carried out by Nommik and Popovic (1971), Overrein (1968; 1969; 1970a; 1970b; 1971a; 1971b; 1972a; 1972b) and Popovic and Nommik (1972) in Scandinavia and by Van Cleve and White (1980) and Weber and Van Cleve

(1981) in interior Alaska.

Hypothesis and Objective

Knowledge has been defined by Fretwell (1975) as what we think we know about truth. As such, knowledge is always an imperfect assessment and hence subject to revision and improvement. One very successful approach to improving our knowledge has been the use of the hypothetico-deductive method whereby a tentative supposition is checked by direct experimental investigation.

Within the framework of the central objective, namely to describe the nitrogen dynamics through the forest floor and moss layers of interior Alaskan black spruce ecosystems, the following hypothesis was formulated: nitrogen flow in the ecosystem compartment under investigation is related to environmental constraints unique to the area, specifically, temperature and moisture regimes as well as organic matter quality. To achieve the objective ^{15}N was used and because of the importance of NH_4-N and NO_3-N in plant nutrition and the limiting nature of these nutrients to plant production in black spruce ecosystems, they were selected as the precursor pools to introduce the label into the system.

LOCATION

The study area is located in the Yukon-Tanana Uplands physiographic province of Alaska, an area of relatively gentle relief with rounded ridges oriented in a northeast-southwest direction. Geologically, the area is characterized by unglaciated Precambrian schist and gneiss bedrock (Johnson and Hartman, 1971; Viereck and Dyrness, 1979). In the vicinity of Fairbanks the Uplands are almost everywhere covered by a mantle of micaceous loess laid down by wind from the outwash plains of the Tanana Valley (Péwé 1955). The study area lies within the zone of discontinuous permafrost (Johnson and Hartman, 1971). Soils encountered in this study are of the Saulich silt loam series, a Histic Pergelic Cryaquept over permafrost and an Alfic Cryochrept over permafrost-free terrain (Table 1).

Climatically, the region is continental in character. Average annual precipitation in the vicinity is 28.6 cm. Almost 19.0 cm of this falls as rain during May to September, the remainder is snow. The annual means of minimum, maximum and average air temperatures are: -9.2°C, 2.2°C and -3.5°C, respectively. The average last day of freezing temperatures in the spring is May 21, and the average first occurrence of freezing temperatures in the fall is August 30, resulting in a growing season of approximately 100 days. The warmest month is July, the coldest month is January with recorded temperature extremes of 37°C and -54°C, respectively. The respective average temperatures for these two months are 16°C and -24°C. (U.S. Department of

Table 1. Description of soil profiles underlying two black spruce ecosystems in interior Alaska[1]

Site	Depth (cm)	Horizon	Color	Texture	Stone content
	23.5-12.7	01			
	12.7- 4.1	021			
	4.1- 0	022	very dark brown (10YR 2/2)		
Washington Creek[1]	0-6	A	very dark grayish brown (10YR 3/2) very dark brown (10YR 2/2)	Silt Loam	none
	6-48	C	dark grayish brown (10YR 4/2)	Silt Loam	none
	14-9	01			
	9-3	021			
	3-0	022	dark brown (10YR 3/3)		
Bonanza Creek	0-6	A_1	very dark brown (10YR 2/2)	Silt Loam	none
	6-52	A_3	dark brown (10YR 4/4) olive brown (2.5YR 4/4)	Silt Loam	none
	52-71+	C	yellowish brown (10YR 5/6)	Thoroughly decomposed schist	20% hard stone fragments, mostly quartz

[1]Modified from Dyrness and Grigal (1979)

Commerce, 1977).

Within this area two black spruce stands of similar age were selected, one within permafrost-free and one within permafrost-dominated terrain. The permafrost-free site is located in the Bonanza Creek Experimental Forest about 32 km west of Fairbanks, Alaska, at latitude 64°45' north and longitude 148°15' west. The permafrost-dominated site is located approximately 50 km northwest of Fairbanks at latitude 65°45' north and longitude 147°55' west in the Washington Creek drainage system (Figure 2). Both sites are on a mid-slope position with a southeast exposure at an elevation of 400 m and 350 m at Washington Creek and Bonanza Creek, respectively. The permafrost-dominated site at Washington Creek has a slope of 10° whereas the permafrost-free Bonanza Creek site is on nearly level ground (Table 2).

The dominant vascular understory species in both stands are Vaccinium vitis-idaea L. subsp. minus (Lodd.) Hult. and Ledum palustre L., subsp. groenlandicum (Oeder) Hult. The pteridophyte Equisetum sylvaticum L., is also conspicuous. A nearly continuous moss cover made up of the feather mosses, Hylocomium splendens and Pleurozium schreberi, occupies 80% of the permafrost-free site and 87% of the permafrost-dominated site. Polytrichum juniperinum Hedw. is a minor component of the moss flora.

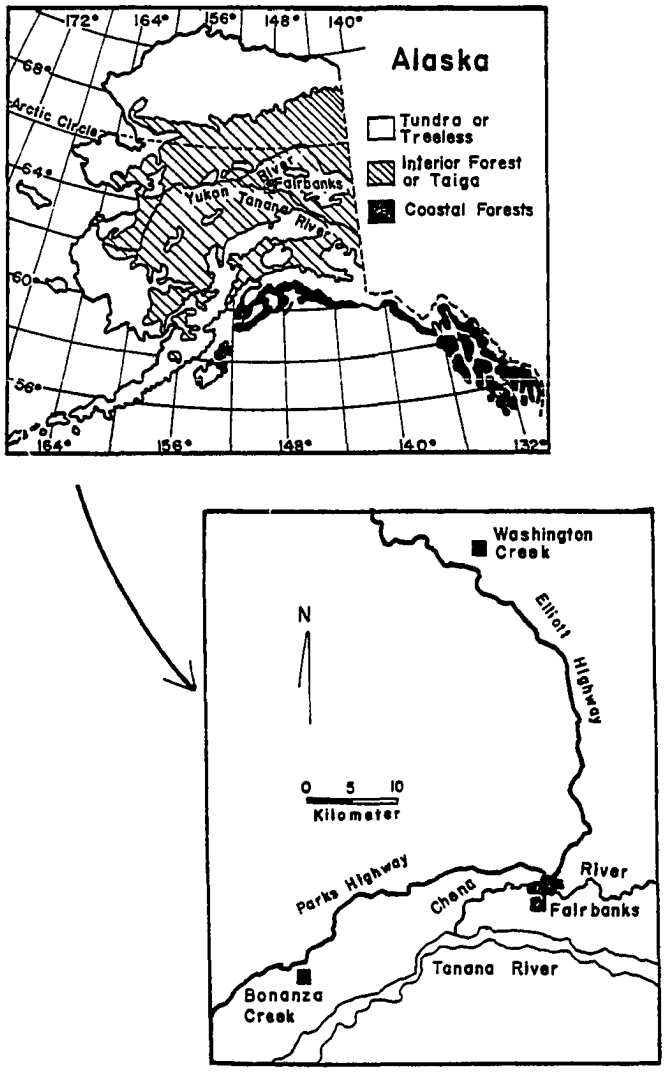

Figure 2. Map of Alaska showing general and specific location of study sites in the interior forest.

Table 2. Summary of selected ecosystem parameters for two interior Alaska black spruce ecosystems[1]

Ecosystem parameter	Washington Creek (Permafrost-dominated)	Bonanza Creek (Permafrost-free)
Age (yr)	138	130
Forest floor depth (cm)	24.0	14.4
Moss cover (%)	98	86
Depth to permafrost (cm)	55	___[2]
Average T°C at 10 cm (May 24 - September 15)	0.5	3.3
Degree days above 0°C (at 10 cm depth)	563	669
Moss production ($g \cdot m^{-2} \cdot yr^{-1}$)	115	125
Vascular plant litterfall ($g \cdot m^{-2} \cdot yr^{-1}$)	39	56
Total above ground tree biomass ($g \cdot m^{-2}$)	5357	10399
Above ground tree production ($g \cdot m^{-2} \cdot yr^{-1}$)	42	80
Fractional annual turnover of the forest floor (k)	0.018	0.019

[1]Data on file with the Forest Soils Laboratory

[2]Permafrost may be present in bedrock

MATERIALS AND METHODS

Field Methods

Each treatment was applied to one 9 m^2 plot. Plots were located to exclude trees in order to have a maximum area available for forest floor sampling. Treatments consisted of ammonium chloride (99 atom % excess ^{15}N) and potassium nitrate (99.3 atom % excess ^{15}N) applied separately to each 9 m^2 plot so as to facilitate labelling of the NH_4-N and NO_3-N pools, respectively. The amounts of isotope applied to each plot were equal to 10, 30, and 100% of the respective available nitrogen pools previously determined for the combined forest floor, i.e., L(01), F(021), and H(022). Application strengths less than 100% of the pool size were included in order to establish what the lowest application strength would be at which nitrogen dynamics could still be detected. Because of the small natural inorganic pools in the forest floor, even the 100% application amounted to less than 1% of the total (Kjeldahl) nitrogen pool. At the permafrost-free site of Bonanza Creek only 10% of the NH_4-N pool could be labelled. The relatively large NH_4-N pool on this site (834 mg $\cdot$ m^{-2}) made application of the isotope at the rate of 30 and 100% prohibitive in terms of isotope costs. Quantities of isotope applied to the forest floor of both sites are shown in Table 3.

The isotopes, dissolved in distilled water, were sprayed as uniformly as possible on the moss covered surface of the respective plots using separate pressure spray cans for each of the two precursors.

Table 3. Rates of isotope application to separate plots on two black spruce sites

Application strength (% of available pool size)	Weight of isotope ($mg \cdot m^{-2}$)** Bonanza Creek		Washington Creek	
	$^{15}NH_4Cl$	$K^{15}NO_3$	$^{15}NH_4Cl$	$K^{15}NO_3$
10	247.85	7.53	31.04	10.18
30	*	22.59	93.12	30.54
100	*	72.25	310.40	101.81

*No treatment

**The amount of $^{15}NH_4$-N in $^{15}NH_4Cl$ and the amount of $^{15}NO_3$-N in $K^{15}NO_3$ was calculated to allow appropriate labelling of their respective natural pools.

The sequence of plots treated was such that the lowest application plots were established first followed by plots of increasing application strength. Total amount of solution used, including sufficient distilled water for rinsing the spray cans, was equal to 0.25 cm of precipitation, an average rainfall in the area (Van Cleve and White, 1980).

Within each plot 36 points were located on a uniformly spaced m^2 grid (4 sampling points $\cdot$ m^{-2}), assigned consecutive numbers on paper, and randomly selected for sampling in time. For each sampling period, two points were randomly chosen for sample extraction with a 15.2 cm diameter coring tool on each of the separately treated plots. Time between sampling was initially short in order to follow early incorporation of ^{15}N into the nitrogen pools.

Isotope application occurred in late May 1977, designated time zero. Sampling was conducted at time zero and continued throughout the growing season of that year (time 5, 20, 40, 60, and 100 days). Additional forest floor samples were taken, one each in July, August, and September of 1978, as well as in September of 1979. The last sampling was deemed necessary because of the unexpected persistence of ^{15}N in the system.

Samples were taken to the top of the mineral soil and included the moss, vascular understory plants and their roots as well as the forest floor layers. Following sampling, replacement cores were extracted from unlabelled areas adjacent to the plots and fitted into

the holes created during sampling to minimize physical disturbance to the forest floor. Furthermore, boards resting on sawhorses were used as a platform from which sample locations near the center of the plots could be reached. In this way stepping on and thus compacting of the low density forest floor was avoided.

In order to follow possible downward movement of the isotope in the soil solution two 520 cm^2 tension lysimeter plates were installed on separately established 100% application plots for each precursor at Washington Creek. Extension of this experiment to include lower strength application plots and the Bonanza Creek site was prevented by time, cost, and equipment constraints. The lysimeters were installed within each of the two plots beneath the 022 layer prior to application of the isotope in the manner described above. The lysimeters provided constant and continuous suction at 0.1 bar for periods of up to four weeks unless the forest floor dried out. The lysimeter plates (Cole et al., 1961) provided a fairly large, known surface area. The known surface area allowed unit area calculation of solution and hence nutrient flux. The large surface area in contact with the forest floor could be expected to provide representative soil solution samples and may also have aided in the collection of small amounts of solution following relatively minor precipitation events.

Soil solutions were sampled on a weekly basis for only the 1978 growing season. Removal of the plates prior to the onset of freeze-up

and subsequent reinsertion during the following spring would have resulted in physical disruption of the plots as well as possible vertical cross-contamination of forest floor layers with ^{15}N.

Extracted cores and soil solutions were put in plastic bags and transferred to Nalgene bottles, respectively, transported to the laboratory and frozen until further processing.

The weather data was routinely collected by members of the Institute of Nothern Forestry at Washington Creek and by members of the Forest Soils Laboratory at Bonanza Creek.

Laboratory Methods

The first of the two extracted cores per treatment was separated into the following components, upon which chemical analyses were performed: green moss by species, brown moss by species (01), 021 and 022 layers. Green was separated from brown moss since there were established differences in physiologial activity as well as organic nutrient content between these two regions of the moss shoot (Busby et al., 1978; Hicklenton and Oechel, 1976; 1977). Vascular plant debris (litter) trapped in either the green or brown moss matrix was designated "green vascular litter" and "brown vascular litter", respectively and analyzed separately. Vascular plants, insofar as present, including their roots were lumped and treated as one component during chemical analyses. In order to avoid erroneous results from possible contamination of lower forest floor layers by the insertion of the coring tool, the outer 5 mm of the extracted core was removed using surgical

scissors. This material was discarded after dry weight determination. All components were dried at 65°C for 48 hours, weighed for biomass estimation and ground in a Wiley Mill to pass a 40 mesh sieve. The Wiley Mill was cleaned with an industrial vacuum cleaner between samples and all parts exposed to the ground material were wiped off with paper tissue soaked in 95% ethanol.

The ground organic material was subjected to two replications of total (microKjeldahl) nitrogen analysis according to Black et al., (1965). Replicated carbon analysis was carried out by using a Leco induction furnance (Allison et al., 1965). Thus, C/N ratios could be calculated and used as an index of organic matter quality in data interpretation.

Total ^{15}N analysis was carried out on a modified Bendix time-of-flight mass spectrometer located at the Institute of Marine Sciences at the University of Alaska, Fairbanks. The lengthy hypobromite procedure traditionally used to produce the labelled N_2 gas that is passed into the mass spectrometer was modified so that $^{15}N_2$ could be directly introduced into the mass spectrometer from dried and ground samples (Dumas method, Barsdate and Dugdale, 1965). Preliminary tests determined that both methods yielded identical results. In the Dumas method the sample is heated with copper oxide at temperatures in excess of 600°C in a stream of purified carbon dioxide gas. The gases liberated are led over hot copper and then over copper oxide to reduce nitrogen oxides to $^{15}N_2$ and to convert CO to CO_2,

respectively. The CO_2 is removed in a liquid nitrogen trap and the $^{15}N_2$ gas is then bled into the mass spectrometer for isotope ratio analysis. Background atom % excess ^{15}N was determined daily from unlabelled ammonium chloride and subtracted from values obtained for the sample. Standard material of known enrichment was run daily as a check on instrument accuracy. Values reported here are means of peak heights for five scans. The lower limit of isotope detection for the instrument was 0.02 atom % excess ^{15}N.

The second set of cores was used for analysis of NH_4-N, NO_3-N, and soluble organic N (SO-N) pools and the determination of their isotope ratios. Since total ^{15}N detection on plots that had received applications less than 100% of the available pool size was low, after one growing season only cores from 100% treatment plots were used for this step (10% NH_4-N application at Bonanza Creek). Furthermore forest floor components were consolidated to represent only three compartments. Green moss species and their associated vascular litter components were combined to form one component. The same was done for the brown moss layer and 021+022 layers were treated as one forest floor component. One sampling date, September 1978, had to be dropped from the analysis scheme due to sample destruction.

Frozen cores were thawed at 5°C until forest floor layers could be separated and weighed. One subsample was removed for dry weight determination, the other was weighed into a 250 ml Erlenmeyer flask for extraction with 2 N KCl. To obtain KCl extracts, samples were

agitated in the extracting solution for one hour on a mechanical shaker. After shaking the contents of the flask were filtered through Whatman No. 5 filter paper under suction. One aliquot of 50 ml was pipetted into a distillation flask with side arm for NH_4-N and NO_3-N determination according to the MgO-Devarda's alloy method of Bremner (1965). A second aliquot of 25 ml was pipetted into a Kjeldahl flask and subjected to routine Kjeldahl analysis to yield an estimate of SO-N. This N fraction has also been referred to as KCl-extractable Kjeldahl N (Mahendrappa, 1980).

To avoid cross-contamination of samples by retention of ^{15}N in the distillation apparatus, 95% etanol was distilled for 5 minutes as a cleansing agent between sample runs (Bremner and Edwards, 1965; Reeder et al., 1980).

All samples were acidified with several additional drops of dilute standard H_2SO_4 ($\underline{N}$=0.01) after titration to end point. The acidified samples were evaporated to dryness in a forced draft oven at a temperature not exceeding 50°C. The dried material of the respective N fractions was analyzed for isotope ratios as described previously.

Known amounts of soil solution samples were freeze-dried on a Thermovac freeze drying apparatus. This yielded a fine powder which was weighed and analyzed for %C and %N on a Hewlett-Packard 185B C-H-N Analyzer. Isotope ratios of treated soil solution samples were determined using the standard procedures outlined above.

Because of the costly and time consuming nature of ^{15}N analysis

extensive field and laboratory sample replication for isotope ratio determination was avoided in order to accommodate the two black spruce sites and the large number of samples generated from them. Retention of the site-comparison-approach was considered a worthwhile trade off for replicated sampling on only a single black spruce site.

The nitrogen tracer technique requires no control treatments, obviating the need to make certain assumptions regarding the similarity of transformation processes in treated and untreated systems. Each isotope ratio measurement is primary information that can be used without reference to other data, although its usefulness can be enhanced considerably when used in relation to other data (Hauck and Bremner, 1976).

Calculations

All nutrient data were expressed on a unit area basis ($mg \cdot m^{-2}$) as well as on a unit weight basis ($ug \cdot g^{-1}$).

Atom % excess ^{15}N was calculated according to the formula of Bremner (1965):

$$\text{Atom \% excess } {}^{15}N = \frac{100\ R}{2+R} \qquad (1)$$

where $R = \frac{I_{29}}{I_{28}}$ i.e. the ratio of ion currents produced by ion species of mass 29 and 28. A mathematical derivation of this formula was given by Edwards (1978).

The field sampling scheme was designed so as to allow eventual construction of isotope dilution curves for N flux determination

according to Shipley and Clark (1972). The net flux or irreversible disposal of N through a precursor pool (that pool into which the ^{15}N is introduced) can be calculated from the dose of ^{15}N and the area beneath the isotope dilution curve:

$$N = D/(A_1/g_1+A_2/g_2) \quad (2)$$

where N = net flux (mg $N \cdot m^{-2} \cdot day^{-1}$), D = dose of ^{15}N (mg N at the given level of enrichment), A = zero time intercept of the exponent (atom % excess ^{15}N), g = rate constant of each exponent ($days^{-1}$), 1, 2 = exponent number. This equation is based on the Stewart-Hamilton equation and gives an estimate of the net input (or output) to that pool which is labelled and sampled (Shipley and Clark, 1972; Van Cleve and White, 1980).

Total flux can be calculated from the dose of ^{15}N and the rate of disappearance of ^{15}N:

$$T = D[(A_1/(A_1+A_2))g_1 + (A_2/(A_1+A_2))g_2] \quad (3)$$

where T = total flux (mg $N \cdot m^{-2} \cdot day^{-1}$) and D, A, and g are defined above. This equation estimates the entry of all N into the sampled pool, i.e., that entering de novo and that recycled.

The contribution made by the precursor to the product pool (that chemical pool in which ^{15}N can be detected and it is assumed that the ^{15}N has undergone the normal chemical or biological reactions to enter that pool within the system) can be calculated from the ratios

of the areas beneath the product and precursor dilution curves:

$$F = \frac{\text{area under product curve}}{\text{area under precursor curve}}$$

$$= (A'_2/g'_2 + A'_3/g'_3 - A'_1/g'_1)/(A_1/g_1 + A_2/g_2) \quad (4)$$

where F = fraction of product arising from precursor, A' = zero time intercept of each exponent (atom % excess), g' = rate constant of each exponent ($days^{-1}$) and A and g are defined above. The areas under the curve can also be determined by the cutting and weighing technique.

Finally, precursor pool turnover time can be calculated as the pool size divided by the total flux (Equation 3):

$$TT = P/T \quad (5)$$

where TT = turnover time (days), P = pool size (mg $N \cdot m^{-2}$) and T is defined above.

All of the above equations assume steady state conditions for the system under investigation, i.e., the size of each of the pools is assumed to remain constant during the term of the experiment and the sum of entry into each pool is equal to the sum of the losses from that pool. Under steady state conditions, flux rates would furthermore be proportional to the amount of ^{15}N in each pool. Instantaneous and homogeneous mixing of ^{15}N with the precursor pool is also assumed (Shipley and Clark, 1972).

As will be seen later, problems arose with regard to the applicability of these assumptions to the system dynamics studied.

RESULTS AND DISCUSSION

Selected Forest Floor Characteristics of Two Interior Alaska Black Spruce Ecosystems

Biomass, %N, %C and C/N ratios for moss and forest floor components at the two black spruce sites are shown in Table 4 and Table 5. There is no statistically significant between-site difference in the weight of the components situated above the O2l layer as determined by Student's t-test. The weights of the O2l and O22 layers, however, are different on the two sites ($P<0.01$) reflecting the difference in the depth of the organic layers between the stands (24.0 cm at Washington Creek and 14.4 cm at Bonanza Creek). Total forest floor weight at Washington Creek is about 40% lower than determined by Barney and Van Cleve, (1973) and Troth et al., (1976) for black spruce stands in interior Alaska. This could be due to site differences as well as the different method of forest floor component separation employed by these workers. The shallower forest floor at Bonanza Creek in conjunction with a greater amount of annual litter input (55.5 $g \cdot m^{-2} \cdot yr^{-1}$ at Bonanza Creek; 38.8 $g \cdot m^{-2} \cdot yr^{-1}$ at Washington Creek [Van Cleve and Dyrness, 1978]) is largely a function of more favorable conditions of soil temperature, drainage and hence decomposition rates. The difference in %N, %C and C/N ratios (Table 5) reflect these conditions. The higher total N values in the Bonanza Creek components indicate the improved nutritional status of this permafrost-free sit compared to Washington Creek. These values coincide closely with those reported

Table 4. Biomass, %N, %C and C/N ratios for feather moss and forest floor components at the permafrost-dominated Washington Creek site (± S.E.). Values are averages for all sampling days.

Component	Dry Weight (g/m^2)	%N	%C	C/N	Sample Size
green *Hylocomium splendens*	47.81 ± 6.98	0.59 ± 0.02	43.63 ± 1.10	73.91 ± 3.47	14
brown *Hylocomium splendens*	27.44 ± 4.84	0.52 ± 0.03	42.58 ± 0.30	83.34 ± 4.53	14
green *Pleurozium schreberi*	155.62 ± 12.69	0.57 ± 0.03	42.62 ± 0.18	77.53 ± 3.09	20
brown *Pleurozium schreberi*	118.85 ± 11.98	0.54 ± 0.03	42.41 ± 0.28	84.14 ± 4.87	20
green vascular litter	51.77 ± 8.13	0.57 ± 0.03	46.14 ± 0.76	84.43 ± 5.17	20
brown vascular litter	27.31 ± 2.61	0.64 ± 0.03	47.74 ± 0.33	77.63 ± 3.47	20
vascular plants	27.90 ± 8.62	0.68 ± 0.06	48.08 ± 0.36	74.30 ± 7.42	6
021	1532.72 ± 168.8	0.73 ± 0.03	45.25 ± 0.34	62.96 ± 2.46	20
022	3708.40 ± 227.06	0.74 ± 0.02	46.24 ± 0.33	62.76 ± 1.62	20

Table 5. Biomass, %N, %C and C/N ratios for feather moss and forest floor components at the permafrost-free Bonanza Creek site (± S.E.). Values are averages for all sampling days.

Component	Dry Weight (g/m^2)	%N	%C	C/N	Sample Size
green *Hylocomium splendens*	44.60 ± 12.04	0.83 ± 0.08*	40.75 ± 0.24*	50.95 ± 4.43*	6
brown *Hylocomium splendens*	16.23 ± 6.92	0.72 ± 0.07*	39.77 ± 1.17*	54.96 ± 3.84*	6
green *Pleurozium schreberi*	205.02 ± 17.02	0.76 ± 0.03*	40.90 ± 0.29*	55.07 ± 1.97*	20
brown *Pleurozium schreberi*	116.14 ± 15.69	0.58 ± 0.02*	40.76 ± 0.68*	72.46 ± 3.51*	20
green vascular litter	68.21 ± 9.69	0.73 ± 0.03*	45.46 ± 0.66	66.00 ± 4.05*	20
brown vascular litter	37.54 ± 4.50	0.72 ± 0.03*	46.61 ± 0.52	66.22 ± 2.78*	19
vascular plants	34.38 ± 10.58	1.01 ± 0.06*	47.50 ± 1.05	47.90 ± 2.78*	8
021	990.74 ± 118.83*	0.98 ± 0.06*	42.37 ± 0.77*	56.15 ± 3.08*	20
022	3173.48 ± 319.27*	1.18 ± 0.03*	43.10 ± 0.39*	36.87 ± 1.04*	20

*Significant between site difference ($P<0.01$)

by Troth et al., (1976) for black spruce stands on varying permafrost-free topographic positions in interior Alaska. The total N values at Washington Creek are slightly lower than those reported by Troth et al., (1976) for their permafrost-dominated sites. The lower %N values at Washington Creek are probably due to permafrost-mediated unfavorable decomposition and nutrient cycling regimes on this site. Consistent with this interpretation is the higher % carbon in the moss and organic layers of the forest floor at Washington Creek, as well as the wider C/N ratios. Carbon/N ratios at Washington Creek are approximately two times higher than reported elsewhere for black spruce ecosystems and between 12 and 70% higher than at Bonanza Creek. Carbon/N ratios at the Bonanza Creek site coincide more closely with the literature (Troth et al., 1976; Weetman and Timmer, 1967). Nömmik and Popovic (1971) consider material with C/N ratios in excess of 40 to be indicative of low decomposition rates. Similarly, Van Cleve (1974), studying organic matter quality in relation to decomposition in circumpolar tundra and taiga sites reported that narrower initial C/N ratios were reflected by more rapid decomposition for a wide range of organic matter. He determined that with respect to substrate quality and decomposition, narrower C/N ratios reflect higher concentrations of readily metabolizable substances such as lipids and starch. The threshold for drastically reduced potential decomposibility of introduced organic matter was around C/N = 80, a value approached or even exceeded by moss and forest floor components at the Washington Creek site (Table 4).

In the interior of Alaska both permafrost-free and permafrost-dominated black spruce sites are clearly examples of ecosystems with slowly decomposing forest floors. However, if ranked in an order of decreasing decomposition rates, permafrost-dominated black spruce ecosystems would be at an even lower position than permafrost-free systems at the same stage of ecosystem development because of the reduced soil temperature regime. Thus, the number of degree days accumulated above 0°C for a depth of 10 cm in the forest floor during the period of May through September 1977 was 669 on permafrost-free and 563 on permafrost-dominated black spruce sites. The difference in degree days between the two sites is reflected by a difference in forest floor thickness and aboveground whole tree biomass. At Washington Creek forest floor depth is >20 cm whereas at Bonanza Creek it is only 14 cm. This has resulted from greater fractional annual turnover of the forest floor at the permafrost-free site (k=0.73) compared to the permafrost-dominated site (k=0.45) (Van Cleve and Dyrness, 1978). These substrate quality controls appear to exert a powerful influence over tree biomass and production. Total aboveground tree biomass and average aboveground tree production are 5357 g/m^2 and 42 g/m^2 respectively for the permafrost-dominated site compared to 10399 g/m^2 and 80 g/m^2 respectively at the permafrost-free site (Van Cleve and Dyrness, 1978). In comparison, more productive non-black spruce ecosystems in the Yukon-Tanana Uplands such as birch, aspen and white spruce characterized by higher tree production

rates and located on more favorable sites with respect to soil temperature, moisture and drainage usually accumulate degree days in excess of 1000 during the same period of time. These sites have greater total nitrogen concentration (1.90 - 2.40% N) and narrower C/N ratios (18.8 - 26.6) in the forest floor organic layers. Troth et al., (1976) concluded that this indicated not only more favorable conditions for microbial decomposition, but also more rapid return of available nutrients to the soil organic layers. An added site ameliorating factor on the warmer, better drained sites is the frequent presence of Alnus. Its actinorhizal nature ensures continuous addition of N to the system through nitrogen fixation. The frequency of Alnus is greatly reduced at this stage of ecosystem development in the permafrost-free as well as permafrost-dominated black spruce vegetation types. Therefore, nitrogen addition by means of actinorhizal association can be expected to be greatly reduced. Most of the nitrogen accretion through biological fixation is contributed by blue-green algae growing epiphytically with the mosses (Billington and Alexander, 1978) and symbiotically with lichens such as Peltigera aphthosa (L.)Willd. (Kallio et al., 1976).

Isotope Distribution and Recovery of Three Application Strengths in Black Spruce Forest Floor Components

The determination of ^{15}N incorporated into the total (Kjeldahl) nitrogen pool of the selected forest floor components from the two precursor pools represented the intial step in the attempt to

describe nitrogen dynamics in this black spruce ecosystem compartment. The results obtained provided a first insight into the behavior of the isotopic tracer in moss and forest floor layers and allowed an evaluation of the relative suitability of the three application strengths (10, 30, and 100% of the available pool sizes) to attaining the stated objectives of the study. As there was no significant difference in atom % excess ^{15}N between the feather moss species encountered (green as well as brown portions) and between 021 and 022 layers, they are shown as "green moss", "brown moss", and "021+022", respectively.

From Figs. 3 through 12 it becomes immediately clear that over a two-year period little incorporation of ^{15}N has taken place in the 021+022 layer of permafrost-free as well as permafrost-dominated stands on all treatments regardless of precursor. The bulk of the isotope remained in the green moss and green vascular litter and, to a lesser extent, in the brown moss and associated litter components. The green/brown feather moss isotope distribution pattern could be expected in light of an earlier study which reported higher organic nutrient contents such as total carbohydrates and sugars in the green portion of the moss (Dicranium fuscescens Turn. in subarctic Quebec, Canada [Hicklenton and Oechel, 1977]). These workers further concluded that little evidence existed for active translocation of nutrients downward from green shoot into the brown portion.

Re-translocation within green segments of the moss shoot has, however, been shown to occur. Skre and Oechel (1979, 1981) were able to

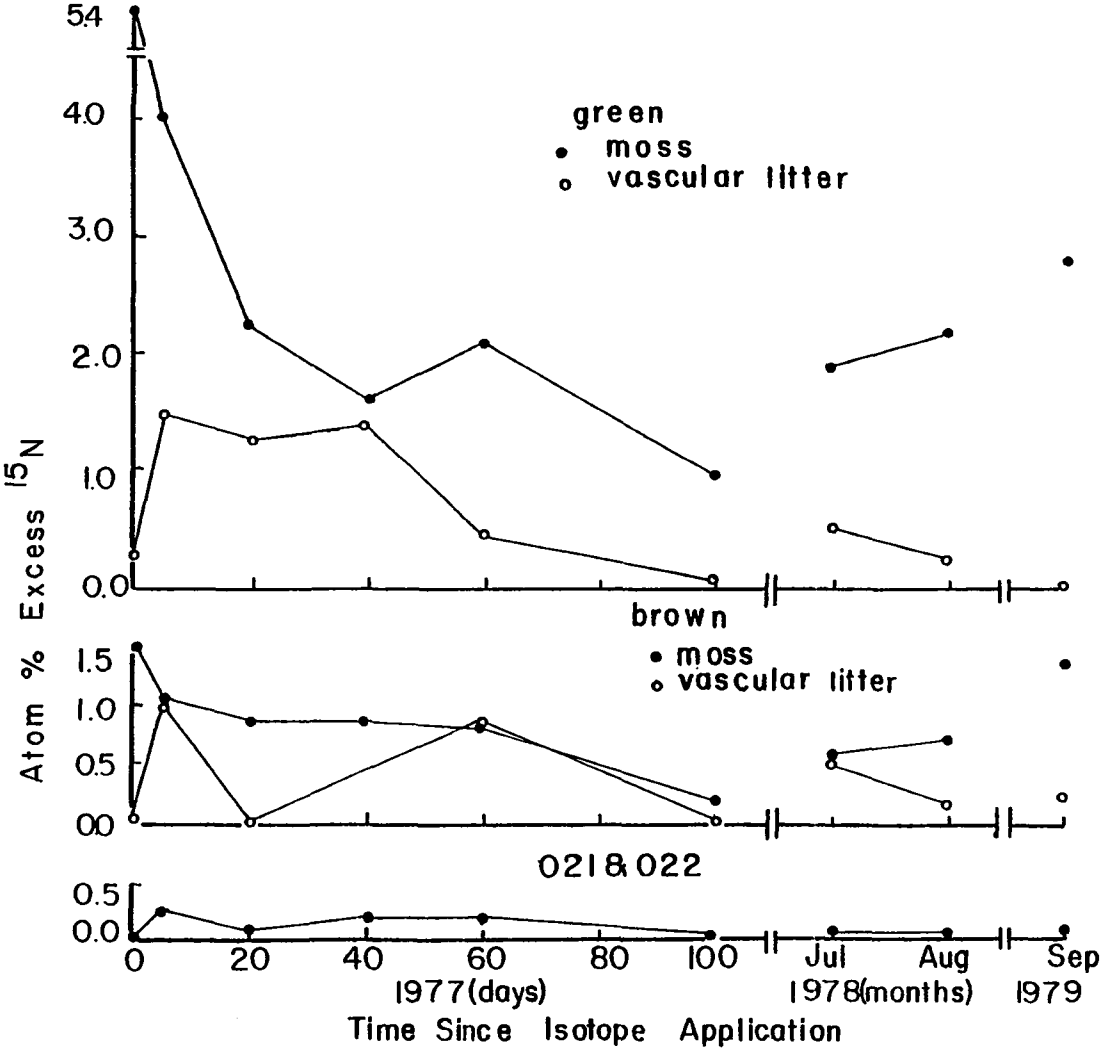

Figure 3. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-dominated site (100% $^{15}NH_4Cl$ application)

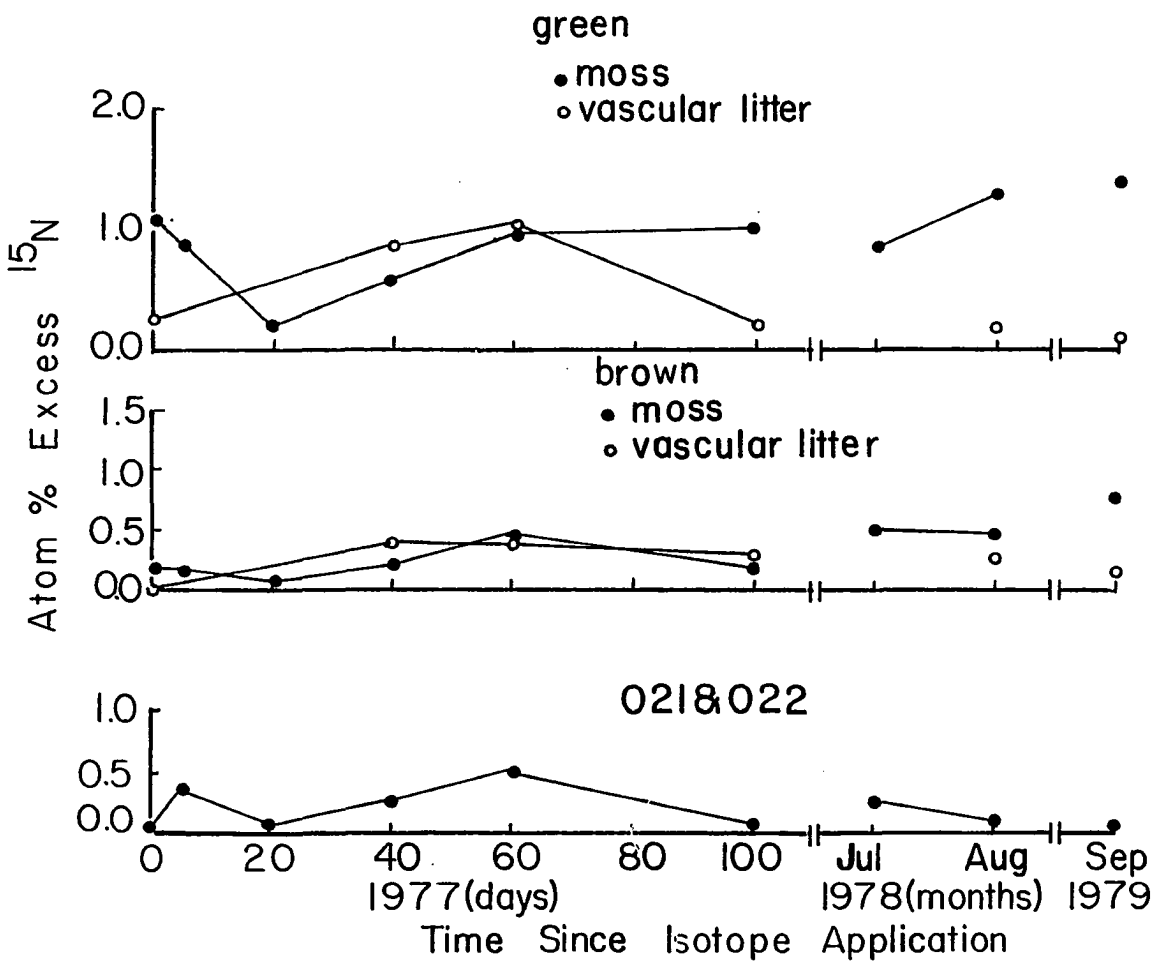

Figure 4. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-dominated site (30% $^{15}NH_4Cl$ application)

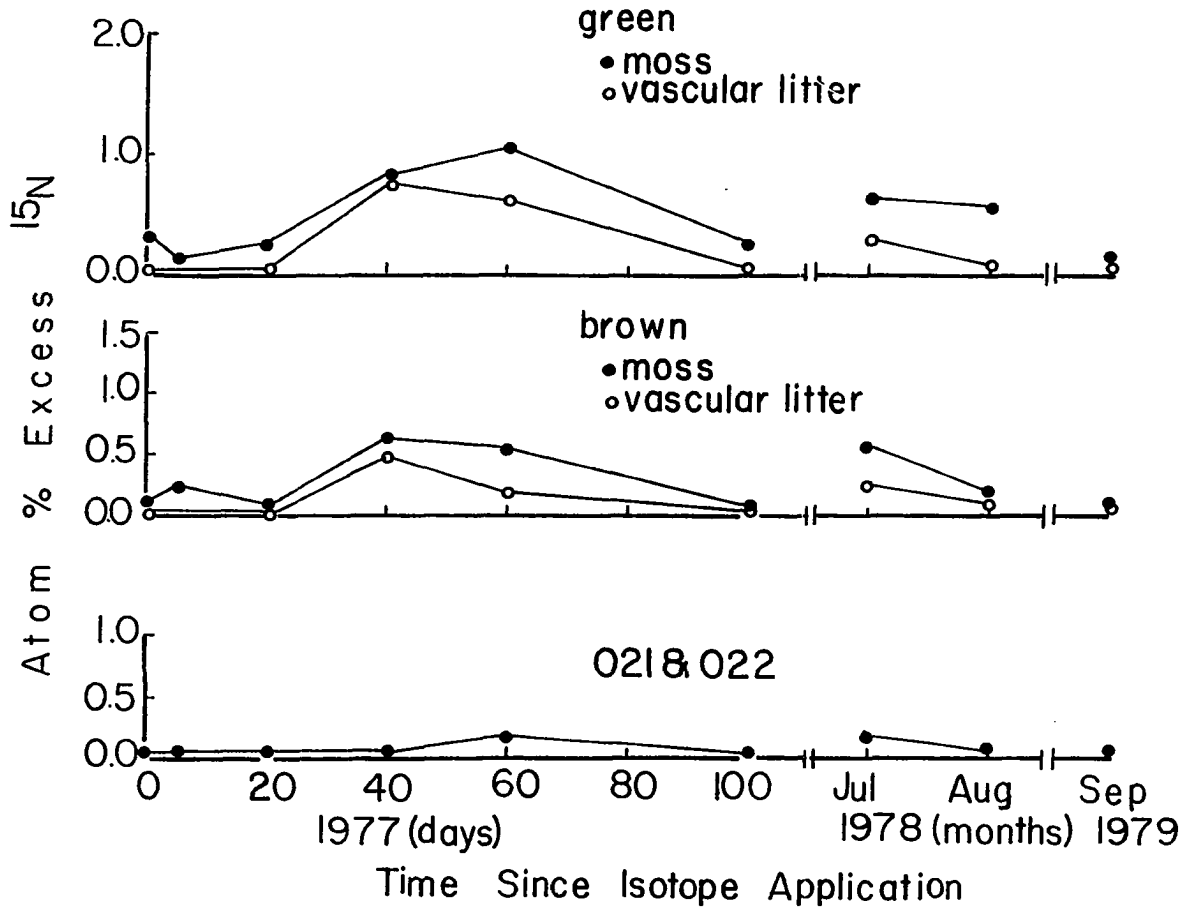

Figure 5. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-dominated site (10% $^{15}NH_4Cl$ application)

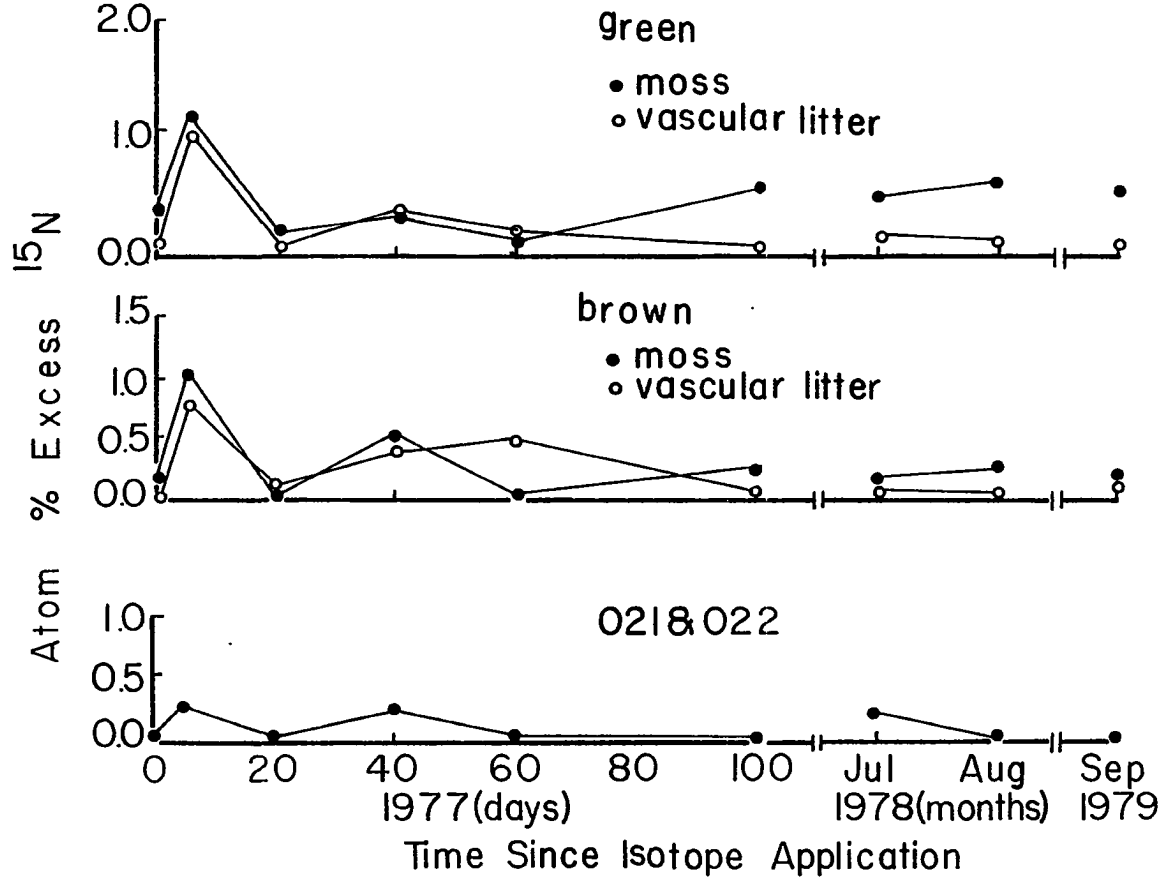

Figure 6. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-dominated site (100% $K^{15}NO_3$ application)

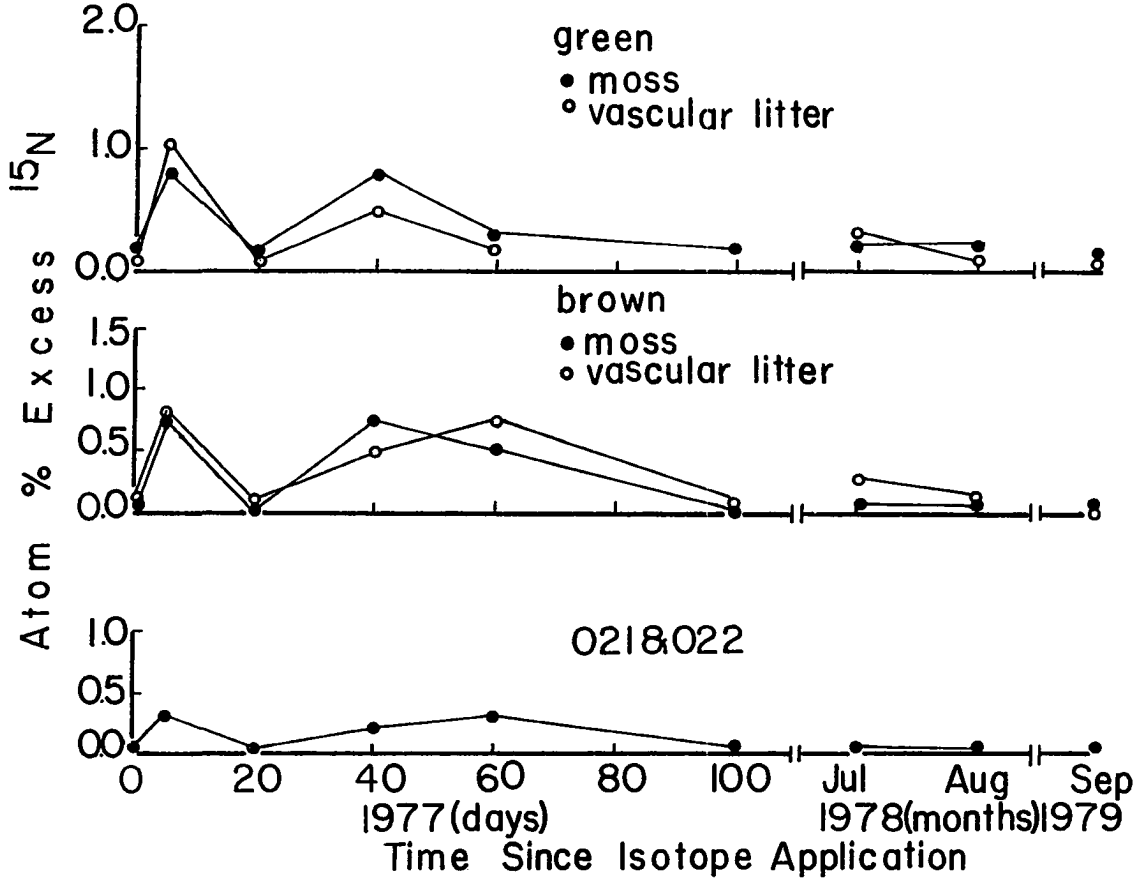

Figure 7. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-dominated site (30% $K^{15}NO_3$ application)

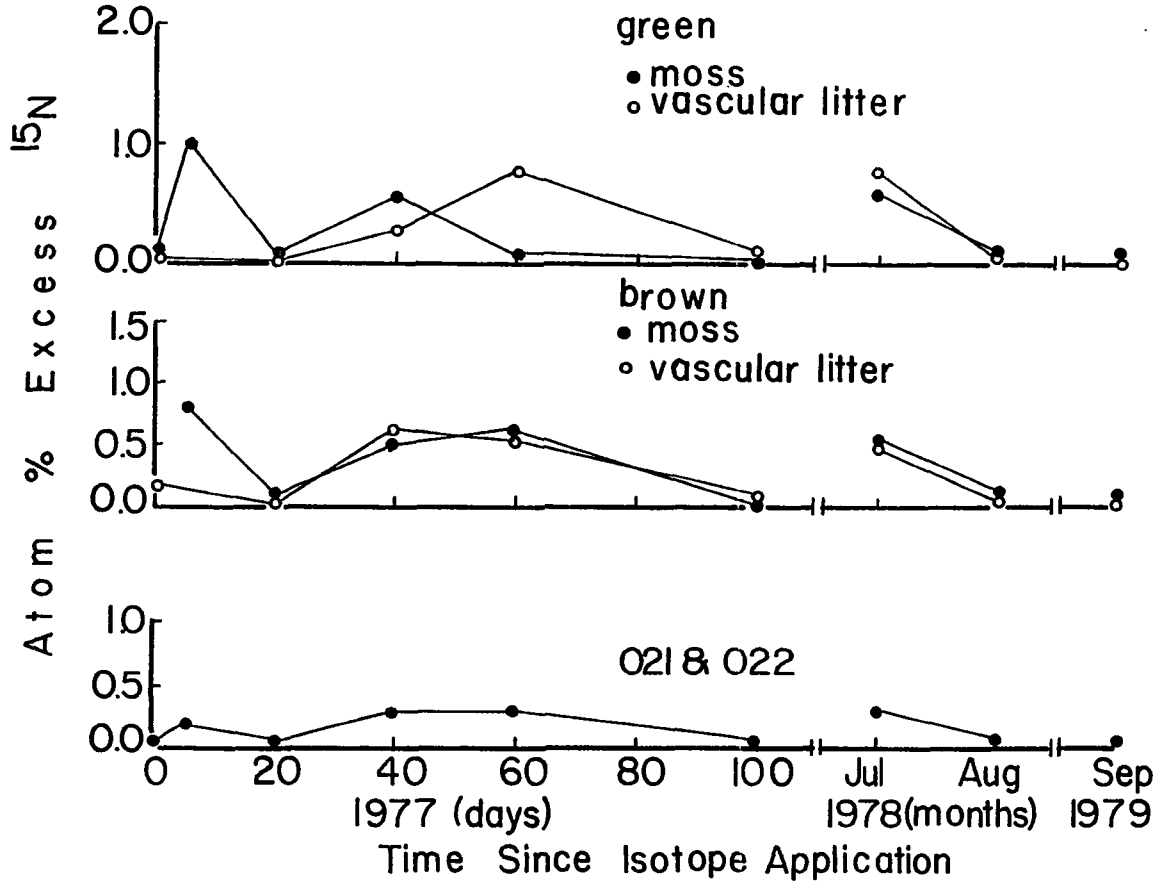

Figure 8. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-dominated site (10% $K^{15}NO_3$ application)

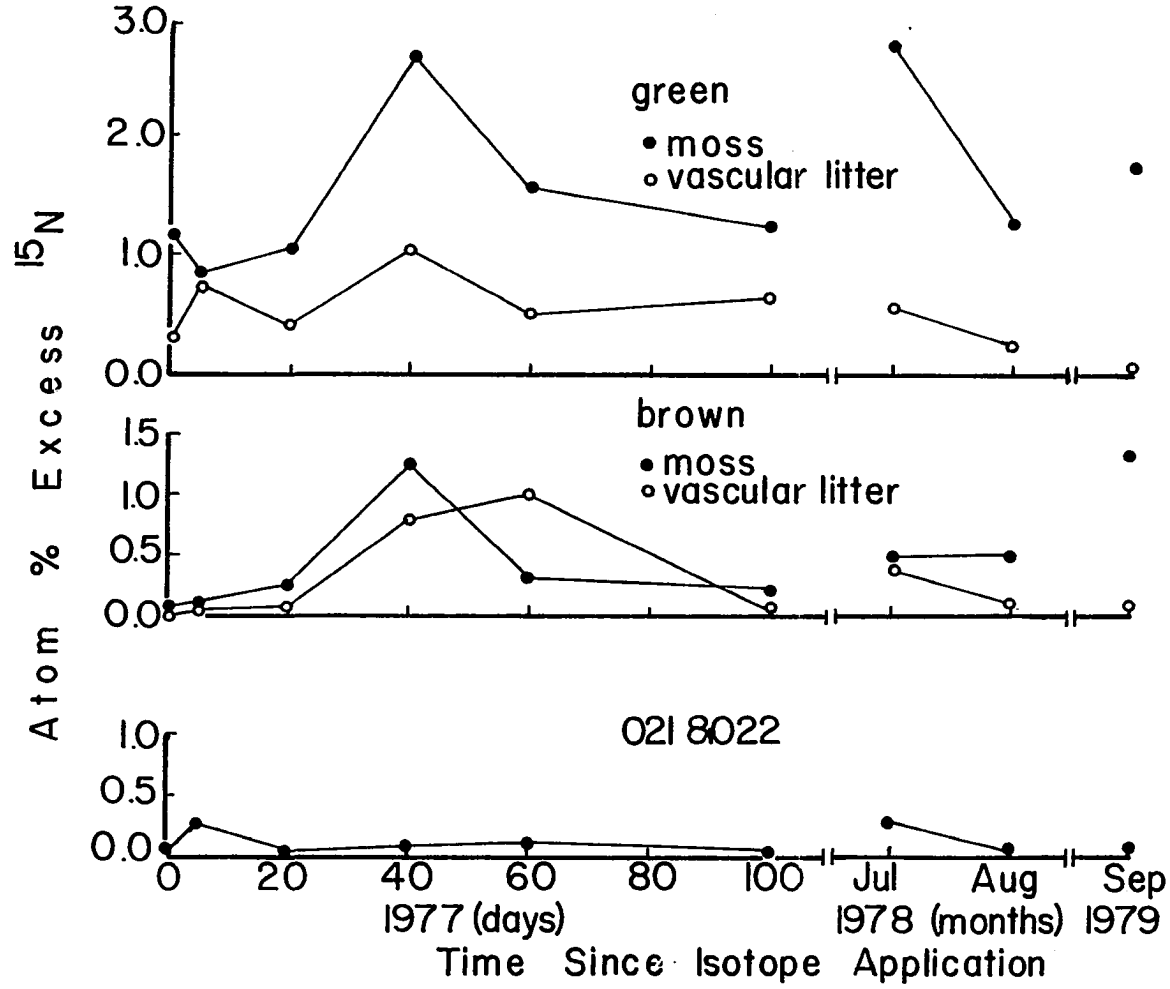

Figure 9. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-free site (10% $^{15}NH_4Cl$ application)

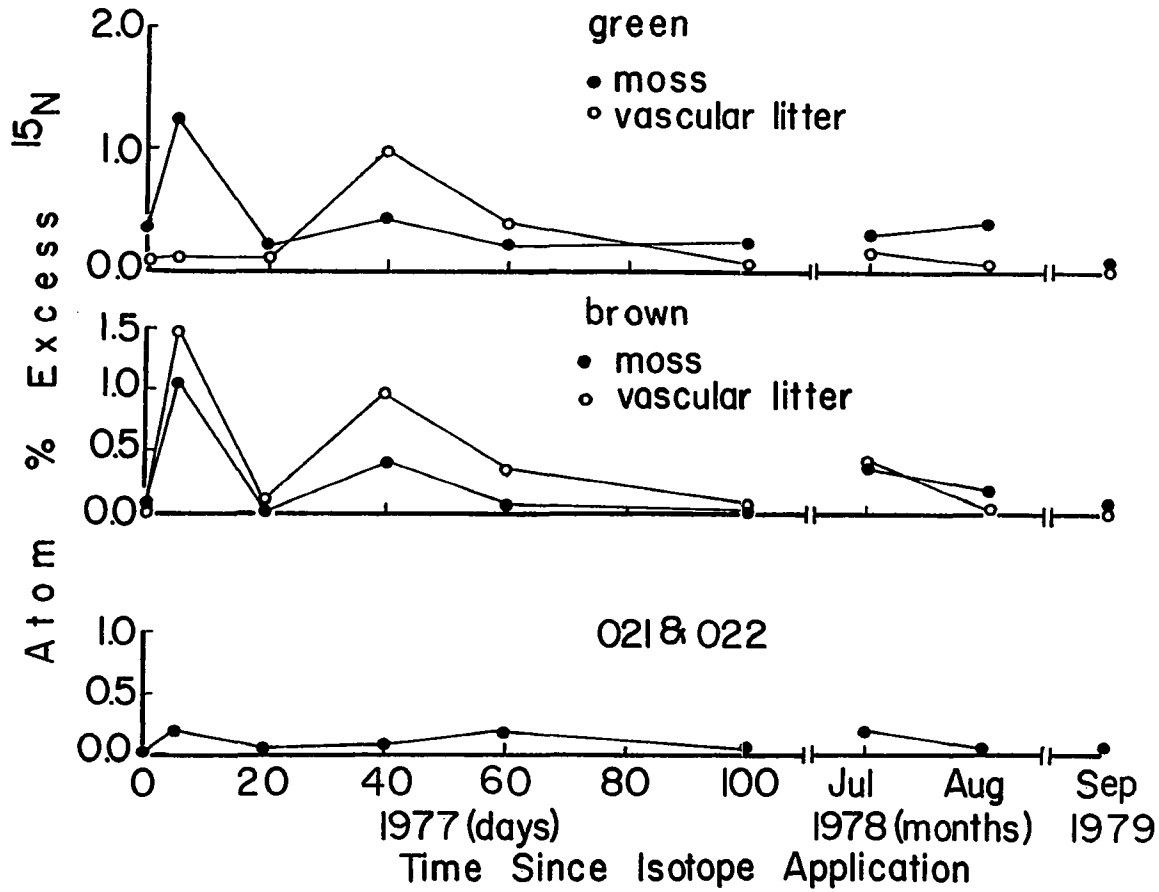

Figure 10. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-free site (100% $K^{15}NO_3$ application)

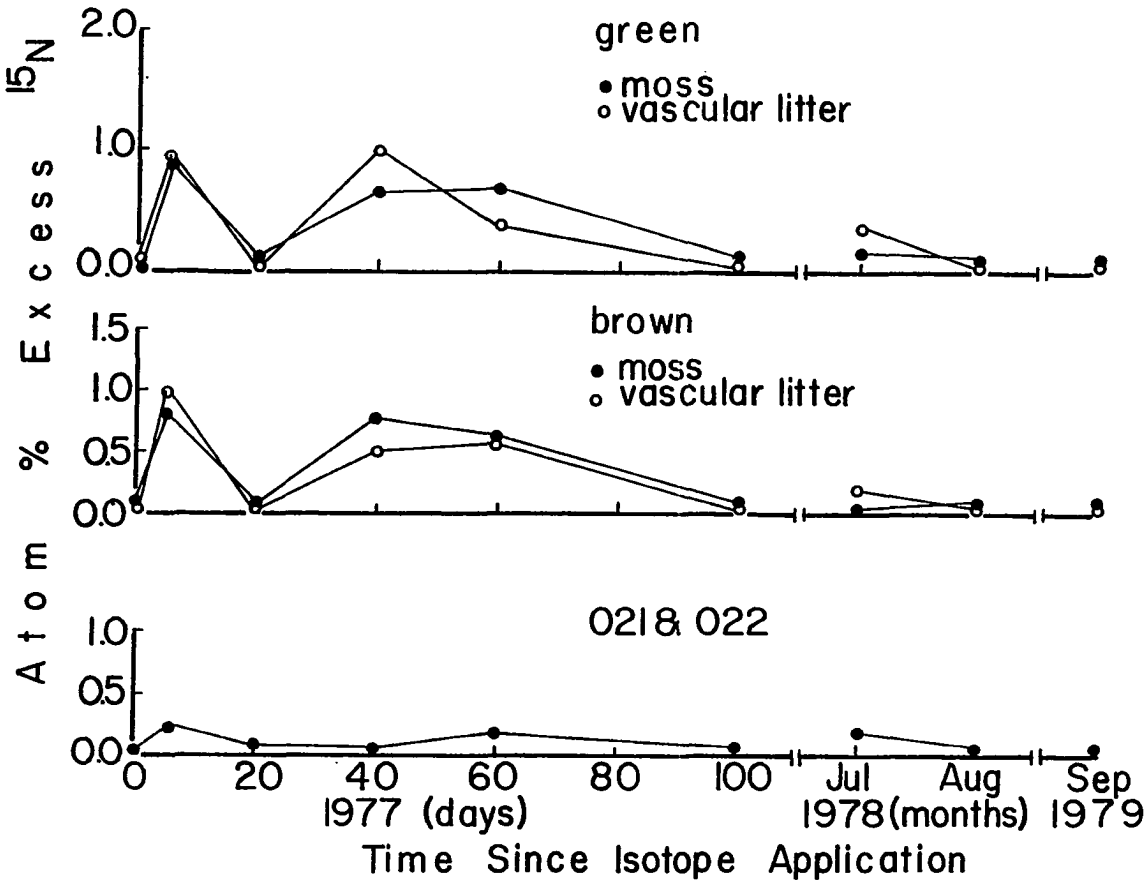

Figure 11. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-free site (30% $K^{15}NO_3$ application)

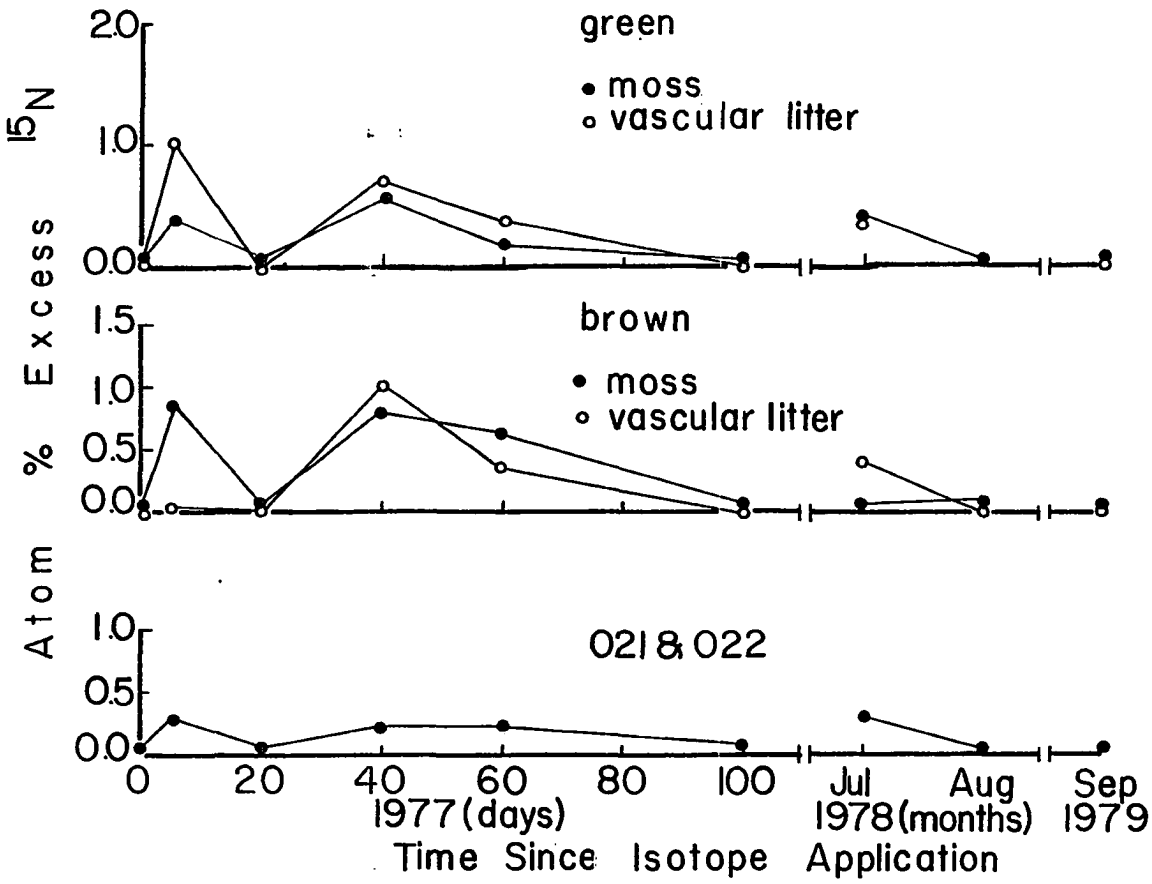

Figure 12. Atom percent excess ^{15}N distribution in the forest floor layers of the permafrost-free site (10% $K^{15}NO_3$ application)

separate four green moss age classes and determined that, at least in the case of Hylocomium splendens, nitrogen was translocated from older to new green tissue (Skre and Oechel, 1979). This could well represent an adaptive strategy to a nutrient limiting environment whereby the resource in short supply, in this case nitrogen, is conserved in growing tissue as green moss senesces and becomes physiologically inactive brown moss.

The decrease in ^{15}N concentration over time results from mixing of the ^{15}N-enriched tracer with natural N sources containing less of the heavy isotope and is referred to an isotope dilution (Edwards, 1978). Isotope concentration immediately after application was highest in the green moss of the 100% $^{15}NH_4Cl$ treatment at Washington Creek, as would be expected after surface application of ^{15}N. Also, isotope dilution trends were most clearly defined on this treatment (Fig. 3). Uptake of ^{15}N by vascular understory plants at Washington Creek was low on all treatments compared to the ^{15}N retained by green and brown moss layers and their associated litter components, but vascular plant uptake could nevertheless have contributed to the observed isotope dilution in the feather moss layers (Figs. 3 through 8). The vascular understory species encountered during sampling were invariably the ericaceous plants Vaccinium vitis-idaea and/or Ledum palustre ssp. groenlandicum. Because of the evergreen habit of these woody shrubs their atom % excess ^{15}N content in the year after the initial isotope

application is a combination of original uptake and overwinter storage, as well as renewed incorporation of ^{15}N during the subsequent growing season. Low levels of enrichment in the vascular plant component of the forest floor are probably a reflection of the low levels of enrichment in the combined 021+022 layer, the major rooting medium of vascular plants on permafrost-dominated black spruce sites (Viereck, 1970b). The green and brown moss layers thus appear to act as a filtering agent for ^{15}N contained in solution on its downward migration through the forest floor profile. Rinne and Barclay-Estrup, (1980) and Ruhling and Tyler, (1970), studying heavy metal contents of feather mosses near smelter operations, similarly found that Pleurozium schreberi and Hylocomium splendens have a considerable capacity for sorption of metal ions from such dilute solutions as tree canopy run-off.

The ability of the feather mosses to retain the applied ^{15}N is best demonstrated on the 100% $^{15}NH_4Cl$ treatment at Washington Creek (Fig. 3) where 90% of the total tracer that could be recovered at the end of the second growing season was contained in green and brown moss components. On the 30 and 10% $^{15}NH_4Cl$ treatments at Washington Creek (Figs. 4 and 5) much of the same observation was made, with 88 and 70% moss retention of recoverable total ^{15}N, respectively, in September of 1978. Absolute values for atom % excess ^{15}N in all compartments, however, were lower on these two treatments compared to the 100% application because of reduced application rates.

The pattern of total ^{15}N retention on the $K^{15}NO_3$ treated plots at Washington Creek was comparable to that of the $^{15}NH_4Cl$ treated plots (Figs. 6 through 8). The feather moss components retained 76, 72, and 45% of the tracer N that could be recovered at the end of two growing seasons on 100, 30, and 10% application treatments, respectively. The lower levels of retention of this precursor at the end of the experimental period, compared to $^{15}NH_4Cl$, is probably related to the greater mobility in the anionic form and to the fact that it may have been held less firmly on exchange sites than the $^{15}NH_4$ cation. In a study on ion exchange in Sphagnum, Clymo (1963) determined that anion exchange ability is less than 0.0026 meq$\cdot g^{-1}$ dry weight compared with about 1.2 meq$\cdot g^{-1}$ dry weight for cations.

Atom % excess ^{15}N values at the end of the second year are in the order: 100 > 30 > 10% $K^{15}NO_3$ application, as was the case on the $^{15}NH_4Cl$ treated plots, but are lower than atom % excess ^{15}N values on the $^{15}NH_4Cl$ treated plots when compared treatment by treatment. The lower atom % excess ^{15}N values on all $K^{15}NO_3$ treatments are, of course, a function of the smaller forest floor NO_3-N pool that had to be labelled. The dominant form of available N in interior Alaska black spruce ecosystems is NH_4-N (Van Cleve et al., 1981). At Washington Creek the pool size of the combined forest floor (021+022 layers) is 104 mg$\cdot m^{-2}$ and 62 mg$\cdot m^{-2}$ for NH_4-N and NO_3-N, respectively; at Bonanza Creek these values are 833 mg$\cdot m^{-2}$ and 46 mg$\cdot m^{-2}$, respectively. The highest amount of isotopic label, therefore, was injected into the 100% $^{15}NH_4$-N plot at Washington Creek (Fig. 3) since at Bonanza Creek only

10% of the NH_4-N pool could be labelled (Fig. 9) due to prohibitive isotope cost (see MATERIALS AND METHODS).

This brings up a point, regarding application rates, that thus far has been ignored. It is obvious that only the 100% $^{15}NH_4Cl$ application at Washington Creek (Fig. 3) satisfied a commonly made assumption in tracer research - namely, that the label mixes instantaneously and homogeneously within the compartment under investigation (uniform penetration of forest floor layers). None of the other treatments showed a maximum peak in atom % excess ^{15}N at time 0, the day of isotope application. If mixing of label within the green moss layer was indeed instantaneous and homogeneous, atom % excess ^{15}N values should have been highest at time 0 and then decline over time in response to isotope dilution as was the case for the $^{15}NH_4Cl$ application at Washington Creek. Failure of the label to mix immediately within the compartment to which it was applied, i.e., the green moss layer, does not invalidate the findings regarding isotope retention by the feather moss component, but points out a problem related to the acceptance of basic assumptions in tracer research under conditions of the present study. Similar concerns were voiced by Robertson (1957); Wilde (1955), and Wrenshall (1955) working with tracers on the development of mathematical equations to describe transfer rates in biological systems.

At the permafrost-free black spruce site at Bonanza Creek isotope retention trends, two years after application, follow the same pattern as at the permafrost-dominated site at Washington Creek (Figs. 9 through 12). Over 90% of the ^{15}N that could be recovered (based on

atom % excess ^{15}N) on the $^{15}NH_4Cl$ treatment was contained in green and brown feather moss components. On the $K^{15}NO_3$ treated plots isotope retention on 100, 30, and 10% applications were 64, 51, and 56%, respectively.

Checking these data against findings by other workers is difficult because different research objectives necessitate experimental procedures which make meaningful comparisons almost impossible. One problem in this regard refers to the length of the experiment. Most studies using ^{15}N as a tool are of relatively short-term duration, such as incubation studies (Overrein, 1972a; 1970a) which can be terminated in a matter of days. Longer-term studies seldom exceed one growing season except in cases where fertilizer persistence in agricultural systems (Kowalenko and Cameron, 1978; Kowalenko and Ross, 1980) or forested systems (Mead and Pritchett, 1975a; 1975b; Overrein, 1972b) is investigated. Fertilizer experiments commonly employ precursors of low enrichment levels applied at high rates, whereas in this study highly enriched precursors were used (over 95 atom % excess ^{15}N) and applied at low rates (< 1% of the total nitrogen pool of the combined 021+022 layers) in order to avoid any priming effect on the system.

The only other *in situ* study carried out in interior Alaskan forest ecosystems and using highly enriched tracers at low levels of application was conducted by Van Cleve and White (1980) in a 60-year paper birch (*Betula papyrifera* Marsh.) ecosystem. Paper birch ecosystems in interior Alaska represent a stage in ecosystem development that is devoid of the thick feather moss layers and hence

characterized by much improved soil temperature and nutrient cycling regimes compared to black spruce ecosystems. The paper birch study revealed high ^{15}N activity in the combined forest floor layers (01+021+022), lending support to the contention that in black spruce stands the moss layers act as a long-term barrier to nitrogen movement into the 021+022 layers of the forest floor, and that in fact the feather mosses may represent a nutrient sink for nitrogen.

Because of the unexpected persistence of total ^{15}N in the green and brown feather moss components of the forest floor in both permafrost-free and permafrost-dominated stands, one more sample was taken at the end of the third growing season (September 1979) from all 100% application plots (10% $^{15}NH_4Cl$ at Bonanza Creek). The 10 and 30% applications were ignored as they showed levels of enrichment at the end of the second growing season that made it doubtful weather ^{15}N detection would be possible after another year. In this study the usefulness of isotope applications at less than 100% of the available pool size thus seems to be restricted to a time frame of no more than 12 months. Furthermore, as pointed out above, it appears questionable whether low levels of application satisfy the assumption of instantaneous and homogeneous mixing of the introduced label within the compartment.

Table 6 shows atom % excess ^{15}N for all moss and forest floor components 28 months after the original isotope application. Isotope

Table 6. Atom % excess ^{15}N contained in feather moss and forest floor components of permafrost-free and permafrost-dominated black spruce sites 28 months after isotope application (± S.E.)

	Permafrost-free**		Permafrost-dominated	
Component	$^{15}NH_4Cl$ treated	$K^{15}NO_3$ treated	$^{15}NH_4Cl$ treated	$K^{15}NO_3$ treated
green *Hylocomium splendens*	*	*	*	0.28 ± 0.03
brown *Hylocomium splendens*	*	*	*	0.16 ± 0.02
green *Pleurozium schreberi*	1.29 ± 0.01	0.27 ± 0.01	1.31 ± 0.04	0.45 ± 0.03
brown *Pleurozium schreberi*	1.21 ± 0.04	0.23 ± 0.02	0.92 ± 0.02	0.26 ± 0.01
green vascular litter	0.12 ± 0.02	0.06 ± 0.02	0.21 ± 0.02	0.08 ± 0.01
brown vascular litter	0.17 ± 0.01	0.05 ± 0.02	0.21 ± 0.02	0.10 ± 0.01
vascular plants	0.05 ± 0.01	0.08 ± 0.02	0.10 ± 0.02	0.06 ± 0.01
021	0.06 ± 0.02	0.02 ± 0.01	0.07 ± 0.02	0.03 ± 0.01
122	0.00	0.03 ± 0.02	0.00	0.05 ± 0.05

*not present

**on this site $^{15}NH_4Cl$ applied at only 10% of the NH_4-N pool site

dilution has continued to take place, but of the ^{15}N that could be recovered from the whole core, over 90% is now contained in the mosses, regardless of treatment. Vascular plants showed little enrichment, as did the 021+022 layer. Interaction between the feather moss and deeper forest floor layers was apparently kept to a minimum. The question arises as to whether this indicates tight internal nutrient cycling within the feather moss layer or tying-up of nitrogen in unavailable form. The answer can only be provided by isotope analyses of the $^{15}NH_4$-N and $^{15}NO_3$-N pools of the respective ecosystem components to be discussed later, but an indication may have been given by Callaghan, (1980), who studied nutrient allocation patterns in Lycopodium annotinum L. in Scandinavian subarctic birch forests. This non-vascular plant, albeit a pteridophyte, overcomes the nutrient stress of its environment by efficiently synthesizing large energy stores while conserving scarce nutrients through recycling within its almost closed system of interconnected vertical and horizontal segments (Callaghan, 1980).

Natural Nitrogen Distribution in Selected N Pools of Black Spruce Forest Floor Components

The information obtained from the above section aided in the decision to analyze only those samples that were collected from plots treated with 100% of the available pool size. Furthermore, forest floor components were consolidated in order to focus more sharply on the role of the feather mosses vis à vis the 021+022 layer. Thus,

for this part of the study, green Pleurozium schreberi and Hylocomium splendens, plus their associated litter components, were combined for analyses and are, henceforth, treated as one component (green moss). Moss species of the brown layer and their vascular litter components were also combined for analyses (brown moss), as were 021 and 022 layers (021+022). Combining of feather moss species seems justified on the basis that their atom % excess ^{15}N as well as total (Kjeldahl) N values were not significantly different at individual sampling dates (the same was true for 021 and 022 layers) and that the responses of these two feather moss species to various environmental factors are similar (Busby et al., 1980). The vascular litter components are lumped with their respective moss layer components because of their intimate physical association with the mosses.

In addition to the detection of ^{15}N activity in the NH_4-N and NO_3-N pools, the soluble organic N pool (SO-N) was also checked for isotope enrichment by chemical analysis. It was determined by subtracting NH_4-N estimates from the KCl extracted Kjeldahl N. It was decided to investigate this nitrogen pool separately since it had been previously shown to be quite large. Van Cleve and White, (1980) calculated that the SO-N can be 37 times the size of the NO_3-N pool in the forest floor of a 60-year old paper birch ecosystem in interior Alaska. Mahendrappa, (1980) working in eastern Canadian feather moss/black spruce forests determined that this nitrogen pool was consistently larger than the NH_4-N pool and went on to conclude that SO-N may be as good an indicator of potentially available N as KCl-extractable

NH_4-N, but appeared to be less attractive because of the additional digestion procedure during sample analysis. The SO-N pool probably consists of root exudates, extracellular microbial enzymes and N incorporated in microbial tissue which is released as a result of turnover of the microbial population, or released as a result of lysis of microbial tissue during sample extraction with 2N KCl (Van Cleve and White, 1980).

Residual organic N (RO-N), representing those N fractions that are more resistant to the mineralization process, was estimated indirectly by subtracting SO-N + NH_4-N + NO_3-N from total (Kjeldahl) N. Like total N it can be considered a sink for mobile forms of N during mineralization-immobiliation reactions.

Table 7 shows the nitrogen concentration in the various natural pools as determinated for the $^{15}NH_4Cl$ application plots on both permafrost-free and permafrost-dominated sites. The total N pool, containing the largest amount of N by definition, was followed in generally decreasing order by RO-N, SO-N, NH_4-N, and NO_3-N. This relationship remained consistent for all three forest floor layers examined on both sites.

Natural variation in N pool sizes is to be expected since soils in general are considered to be a notoriously heterogeneous medium to work with (Keeney, 1980). In addition, nitrogen content in the forest floor would be affected by seasonal variations in biological activity due to changing temperature and precipitation patterns. Haines and Cleveland (1981) point out that careful consideration must

Table 7. Nitrogen concentration in selected floor components on the $^{15}NH_4Cl$ treated plot of permafrost-free and permafrost-dominated black spruce sites ($ug \cdot g^{-1}$).

Time after application	Site	Green moss					Brown Moss					021+022				
		Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N
	W. Cr.	5400	5236	130	21	13	4350	4171	149	26	4	6400	6238	131	27	4
0	B. Cr	9800	9547	215	33	5	6800	6510	218	62	10	11550	11159	249	134	8
	W. Cr.	5400	5279	105	7	9	4400	4270	101	22	7	7550	7360	144	38	8
5	B. Cr.	7300	7231	236	34	9	5300	4976	278	38	8	10650	10427	177	45	8
	W. Cr.	6200	5905	239	41	15	6300	5203	172	9	16	8100	8010	70	14	6
20	B. Cr.	8500	8225	204	7	4	6500	6324	157	11	8	13700	13301	342	52	5
	W. Cr.	5100	4676	397	19	8	4200	3810	343	32	15	7200	6993	178	17	12
40	B. Cr.	5800	5436	327	24	13	5700	5427	213	40	20	10350	9979	264	100	12
	W. Cr.	7350	7129	201	10	10	6550	6331	174	31	14	6750	6362	113	21	9
60	B. Cr.	9100	8782	262	46	10	6800	6553	209	26	12	9900	9512	317	59	12
	W. Cr.	6400	6068	299	23	10	7800	7571	200	20	9	7800	7428	224	140	8
100	B. Cr.	6500	6256	200	35	9	5300	5074	181	31	14	13750	13159	402	177	12
	W. Cr.	7600	7436	137	23	4	7300	7168	114	13	5	9100	8953	122	20	5
Jy 78	B. Cr.	9500	4236	192	66	6	4700	4569	101	23	7	10050	9600	301	142	7
	W. Cr.	6600	6341	215	18	26	5950	5644	243	46	17	7600	7358	167	62	13
Aug 78	B. Cr.	6900	-	447	-	28	4000	3628	278	72	22	9150	8655	312	164	19
	W.Cr.	7550	7401	83	27	39	7000	6855	107	29	9	7700	7594	82	18	6
Sept 79	B.Cr.	7500	7230	216	25	29	5200	4953	197	33	17	11350	10826	438	74	12

be given to sampling intensity if inherent natural seasonal changes in soil chemical or physical properties are to be separated from changes due to a given treatment. These authors calculated sample sizes required to estimate various physical and chemical parameters in five forest soils in southwest Georgia. To estimate the value of a soil property, such as cation exchange capacity within $\pm$ 10 and $\pm$ 5% of the mean with 95% confidence 198 and 789 samples were required, respectively. In another study Quesnel and Luvkulich (1980) determined that 100 samples are needed to estimate forest floor thickness on a mesic site on Vancouver Island, British Columbia, if 95% confidence within 10% of the mean was to be achieved.

The scope of the present study precluded sampling that even remotely approached sampling intensity of this level and resulted in a concomitant increase of variation in the data. Fortescue (1980) aptly noted that a universal constraint to the scientific effort applied for the solution of a problem is availablility of funds and time and that this aspect of the research often dictates the kind of scientific effort used to solve a specific problem.

Comparing all sampling dates on the $^{15}NH_4Cl$ treated plots there is a between-site difference in N concentration of the total N pool of green moss and 021+022 layers ($P<0.05$). At the Bonanza Creek site the total N pool is larger in these two forest floor layers, as could be expected from previous discussion. The 021+022 layer furthermore showed higher values for the SO-N and NH_4-N pools than Washington Creek

($P<0.01$). No significant between-site differences could be detected in the various N pool sizes of the brown moss layer on this treatment.

On the $K^{15}NO_3$ treated plots pool size relationships were similar to those on the $^{15}NH_4Cl$ treated plots (Table 8). Total N represented the largest pool followed in decreasing order by RO-N, SO-N, NH_4-N, and NO_3-N pools. On this treatment the improved nutritional regime of the permafrost-free site at Bonanza Creek appeared, however, to be better defined. Between-site differences existed in all three forest floor layers for total N and SO-N pools ($P<0.01$), Bonanza Creek being characterized by higher values. The NH_4-N pool is larger in the brown moss layer of Bonanza Creek than at Washington Creek ($P<0.05$), but not significantly different in green moss and 021+022 layers on this treatment.

The majority of the pertinent literature expresses soil nutrient content on a unit area basis such as $kg \cdot ha^{-1}$ or $mg \cdot m^{-2}$. This way of data presentation is based on incorporation of the density of a given layer into the calculation. Forest floor bulk density and depth are highly variable (Haines and Cleveland, 1981), even more so in high latitudes because of the presence of permafrost. The permafrost table is uneven and recedes downward during the summer (increase in depth of active layer), representing an added source of variation. Density of forest floor layers examined in this study increased with depth from the very low density green feather moss layer ($0.02\ g \cdot cc^{-1}$) to the more compact 021+022 layer ($0.08\ g \cdot cc^{-1}$) so that for the same hypothetical level of nitrogen in all layers, say 0.8% Kjeldahl N, the 021+022

Table 8. Nitrogen concentration in selected forest floor components on the $K^{15}NO_3$ treated plots of permafrost-free and permafrost-dominated black spruce sites ($ug \cdot g^{-1}$).

Time after application	Site	Green moss					Brown Moss					021+022				
		Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N
	W. Cr.	4850	4670	156	18	5	5150	4937	191	16	6	6550	6368	162	12	8
0	B. Cr.	8200	7976	203	13	8	7500	7202	259	28	11	11300	10910	247	131	12
	W. Cr.	4650	4501	133	9	7	4000	3881	95	14	10	8050	7916	93	36	5
5	B. Cr.	6500	6122	336	30	12	6400	5934	434	24	8	10700	10396	224	71	9
	W. Cr.	4900	4712	168	11	11	6900	6766	121	5	8	8100	7960	106	28	6
20	B. Cr.	9450	9161	266	8	15	7850	7528	301	14	7	12700	12305	324	67	4
	W. Cr.	4500	4183	291	20	6	4200	4014	164	14	8	6850	5728	113	6	3
40	B. Cr.	7300	6813	409	63	15	-	-	674	106	13	12200	11595	502	95	8
	W. Cr.	4750	4447	251	38	14	4550	4411	115	11	13	6000	5825	136	23	16
60	B. Cr.	7900	7459	373	54	14	7000	6743	225	25	7	11350	10933	314	98	5
	W. Cr.	5950	5725	177	42	6	4850	4608	211	31	13	7700	7516	151	24	9
100	B. Cr.	5900	5446	397	36	22	5300	4968	287	34	11	10400	9921	381	84	14
	W. Cr.	5100	4865	202	24	9	4800	4645	135	14	6	6200	6017	122	55	6
Jy 78	B. Cr.	7800	7231	471	81	17	6400	6058	270	37	8	10050	9374	505	164	7
	W. Cr.	4900	4645	218	16	21	3950	3755	150	25	20	6750	6075	250	393	32
Aug 78	B. Cr.	8200	7754	349	67	30	5300	4908	285	92	15	10150	9652	348	138	12
	W. Cr.	5650	5508	72	37	33	5000	4824	110	34	32	7050	6818	158	56	18
Sept 79	B. Cr.	7400	7117	240	13	30	6200	5934	228	29	9	9650	9288	299	50	13

layer would constitute the major source of this nutrient by virtue of its higher density.

So far forest floor nutrient content has been expressed on a unit weight basis. This method of calculation avoids the problem of variability in density within and among layers (Amato and Ladd, 1980; Ladd and Amato, 1980). Either method to calculate nutrient content is valid and, as will be seen later, together they will yield information or point out problem areas which one method alone could not accomplish. Hence, Table 9 and 10, analogous to Table 7 and 8, show the data expressed on a unit area basis. This method of calculation shows that pool sizes can be ranked as before. The largest amount of N is contained in the unavailable forms of the total N and RO-N pools, followed in decreasing order by SO-N, NH_4-N, and NO_3-N pools. This pattern occurs without exception on both $^{15}NH^4Cl$ and $K^{15}NO_3$ treated plots. Between-site differences were more pronounced using unit area calculations since statistically significant differences in N pool sizes occurred more frequently. Thus, on the $K^{15}NO_3$ treated plots the green moss layers at Bonanza Creek shows higher values for all forms of N examined compared to Washington Creek ($P<0.05$). The brown moss layer contained larger amounts of N in the SO-N and NH_4-N pools ($P<0.05$) and the O21+O22 layer had a larger SO-N pool ($P<0.05$). On the $^{15}NH_4Cl$ treated plots at Bonanza Creek green moss contained more N in the total and SO-N pools ($P<0.05$); brown moss and O21+O22 layers had larger SO-N, NH_4-N and NO_3-N pools

Table 9. Nitrogen pool sizes in selected forest floor componets on the $^{15}NH_4Cl$ treated plots of permafrost-free and permafrost-dominated black spruce sites ($mg \cdot m^{-2}$).

Time after application	Site	Green Moss					Brown Moss					021+022				
		Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N
0	W. Cr.	1787	1676	88	14	9	1047	942	87	15	3	34782	33231	1253	259	40
	B. Cr.	3061	2882	152	23	3	890	662	171	49	8	78035	72001	3847	2063	124
5	W. Cr.	2732	2634	85	6	7	1327	1269	45	10	3	30521	28636	1431	375	80
	B. Cr.	2356	2108	210	30	8	1475	1242	200	27	6	32009	29956	1604	404	45
20	W. Cr.	1155	995	130	22	8	627	534	81	4	8	47344	46566	609	117	51
	B. Cr.	1751	1575	168	5	3	761	553	186	13	9	81726	73639	6931	1050	107
40	W. Cr.	1760	1518	223	11	5	996	834	129	12	6	33292	31625	1439	135	93
	B. Cr.	1534	1352	164	12	7	605	444	127	23	12	28844	22210	4696	1806	131
60	W. Cr.	1750	1650	91	5	5	2071	1976	76	14	6	33280	31866	1110	210	94
	B. Cr.	2356	2161	161	28	6	1512	1335	149	18	9	61274	57895	2169	404	79
100	W. Cr.	1573	1394	161	13	6	1436	1349	76	8	4	38013	35640	1426	898	49
	B. Cr.	1618	1451	137	24	6	786	561	180	31	14	84571	80864	2497	1119	91
Jy 78	W. Cr.	1356	1244	93	16	3	1241	1167	64	7	3	38732	37511	1010	168	42
	B. Cr.	3661	3389	198	68	6	1241	1052	146	33	10	48017	43055	3360	1528	75
Aug 78	W. Cr.	1677	1569	90	8	11	1147	932	171	32	12	65827	63950	1297	478	102
	B. Cr.	2693	-	213	-	13	1323	1077	184	48	14	40575	35247	3328	1795	204
Sep 79	W. Cr.	2348	2291	32	11	15	811	736	55	15	5	56757	55606	836	186	56
	B. Cr.	2582	2448	107	13	15	651	500	120	20	10	65788	60332	4548	778	130

Table 10. Nitrogen pool sizes in selected forest floor components on the $K^{15}NO_3$ treated plots of permafrost-free and permafrost-dominated black spruce sites ($mg \cdot m^{-2}$).

Time after application	Site	Green moss					Brown moss					021+022				
		Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-N	Total N	RO-N	SO-N	NH_4-N	NO_3-
0	W. Cr.	1454	1341	98	11	3	960	816	129	11	4	34047	32691	1210	90	58
	B. Cr.	1460	1288	156	10	6	695	571	108	12	5	40611	37928	1697	903	83
5	W. Cr.	1079	968	100	7	5	607	523	66	10	7	53418	51457	1358	533	70
	B. Cr.	1924	1643	250	22	9	1102	815	267	15	5	16161	11400	3510	1108	144
20	W. Cr.	1153	1065	79	5	5	1453	1380	65	3	5	43642	42052	1200	321	70
	B. Cr.	3098	2939	146	4	8	630	496	123	6	5	51882	47492	3604	748	39
40	W. Cr.	1514	1386	117	8	2	591	484	85	8	4	30803	29594	1116	60	34
	B. Cr.	2077	1874	170	26	7	712	231	409	64	8	35948	25135	9003	1684	127
60	W. Cr.	968	830	114	17	6	687	611	63	6	7	24357	23052	1015	169	121
	B. Cr.	3056	2761	249	36	10	1702	1513	165	18	5	63537	60910	1910	683	34
100	W. Cr.	1510	1376	106	25	4	791	632	132	19	8	48419	46889	1257	198	74
	B. Cr.	1472	1132	297	26	16	783	556	196	23	8	34288	32568	1367	302	50
Jy 78	W. Cr.	2038	1927	96	12	4	989	933	49	5	2	22398	19397	2000	910	91
	B. Cr.	1930	1693	195	34	7	1305	1109	168	23	5	29283	26611	2002	546	24
Aug 78	W. Cr.	1415	1300	99	7	9	882	784	75	13	10	27540	22026	2042	3213	260
	B. Cr.	2298	2054	191	37	17	1109	889	160	52	9	22718	18149	3194	1267	108
Sept 78	W. Cr.	1483	1461	12	6	5	864	769	60	18	17	42239	40026	1505	535	173
	W. Cr.	1532	1379	130	7	16	762	644	101	13	4	67558	62375	4208	716	187

at $P<0.01$ and $P<0.05$, respectively. Between-site difference in total and RO-N pools in brown and 021+022 layers was non-significant on either of the two treatments.

Both methods of calculating nutrient content showed that NH_4-N was the predominant form of nitrogen compared to NO_3-N and this relationship was most consistent in the 021+022 layers of both black spruce sites regardless of treatment. The dominance of one of these two forms of nitrogen over the other has received considerable attention in the literature with discussions centered around the strategies of ecosystem development as formulated in the now classical paper by Odum (1969). The central hypothesis of this paper revolves around the premise that young communities have open nutrient cycles and rapid exchanges of nutrients between organisms and their environment, but that in more mature successional stages the cycles become more closed and that exchanges between organisms and their environments become slower. Since then terms such as "leaky" have been used to describe early successional stages as compared to "tight" late successional stages (Lamb, 1980; Montes and Christensen, 1979; Vitousek and Reiners, 1975).

Supporting evidence for this type of ecosystem strategy has been provided by another citation classic (Rice and Pancholy, 1972). These authors found nitrification rates to be low in late successional communities and ascribed the dominance of ammonium over nitrate in these systems to "inhibition of nitrification by climax vegetation".

They argued that this was a logical development in the evolution of an ecosystem since nitrogen leaching losses in the form of the negatively charged NO_3-N ion would be reduced. Furthermore, plant uptake of NH_4-N would conserve plant energy since energy is required to reduce nitrate to nitrite and nitrite to ammonium. In two later papers they proposed that the mechanisms to account for the reduced nitrification rates was related to the production of tannins and tannin derivatives by the climax vegetation which inhibited nitrifying populations of Nitrosomonas and Nitrobacter (Rice and Pancholy, 1973; 1974).

Not all experimental results have necessarily supported the above contentions. Specifically, Vitousek (1977) and Vitousek and Reiners (1975) determined that nitrate concentrations were relatively constant and high in streams draining mature spruce-fire forests in New England. Streams draining immature ecosystems showed low and seasonally variable nitrate concentrations. These authors maintained that nitrification occurs throughout the successional sequence and that the change in nitrate concentration is simply due to a change in ecosystem productivity; early successional stages having high productivity and rapid nitrogen uptake. By contrast, productivity decreases as succession proceeds and less mineralized nitrate is absorbed by the vegetation.

In the literature evidence can be found in support of either of these findings. For example, Montes and Christensen (1979) working in the Piedmont area of North Carolina and Lamb (1980) studying secondary rain forest succession in Australia suggested that inhibition

of nitrification is not an invariable consequence of successional development. Robertson and Vitousek (1981), monitoring nitrification potentials in primary and secondary succession of the Indiana Dunes on the southern edge of Lake Michigan also rejected the hypothesis of progressive inhibition of nitrification in the course of ecological succession. On the other hand, Haines (1977), working in forested areas of South Carolina, Oklahoma, Missouri and North Dakota, Lodhi (1975; 1977; 1978), and Lodhi and Killingbeck (1980) squarely side with the concept of inhibition of nitrification by late successional vegetation.

Whether the low nitrate levels in the black spruce ecosystem under consideration are a function of inhibition of nitrification due to allelopathic effects by the overstory vegetation would require microbial investigations into the species composition of the forest floor in combination with laboratory experimentation to determine possible inhibitory effects of plant litter or leachates on the microbial population. As Vitousek (1977) pointed out, small NO_3-N pools _per se_ are insufficient evidence for inhibition of nitrification. In addition it must be shown that NO_3-N production is also low. For instance, a system in which plants can take up nitrate more rapidly than it can be produced will have small NO_3-N pool sizes, while a system with lower plant uptake and the same nitrification range will have higher pool sizes. A system with a small pool of nitrogen which turns over rapidly may have as much nitrogen cycling through the soil nitrate pool in

a year as a system with a large pool that turns over more slowly (Vitousek, 1977). An added complicating factor is the possibility that plants and decomposers outcompete the nitrifying population for substrate, namely NH_4-N.

By implication, the disparity in nutritional status of the two black spruce stands studied here is therefore not only a reflection of a difference in their static forest floor N pool sizes at any given point in time, but may also reflect different nitrogen flux rates through these pools during a specified time interval.

^{15}N Movement through Selected Pools of Black Spruce Forest Floor Components

Atom % excess ^{15}N determination

As a first approximation to describing ^{15}N movement through the nitrogen pools examined (Total N, RO-N, SO-N, NH_4-N, and NO_3-N) their isotope ratios, expressed as atom % ^{15}N, are shown in Figs. 13 through 16. On the $^{15}NH_4Cl$ treated plot at Washington Creek (Fig. 13) the N pools of the green and brown moss layers remained the most highly labelled over the three year period of investigation compared to the combined 021+022 where atom % excess never exceeded 0.5. If changes in isotope ratios are taken as an indication of the dynamic nature of nitrogen transformations, then the moss layers, notably the green, are most active in this respect. After an initial 5-day isotope dilution in all N pools of the green moss layer ($^{15}NO_3$-N atom % excess ^{15}N stayed constant) the SO-N and NH_4-N pools became increasingly labelled

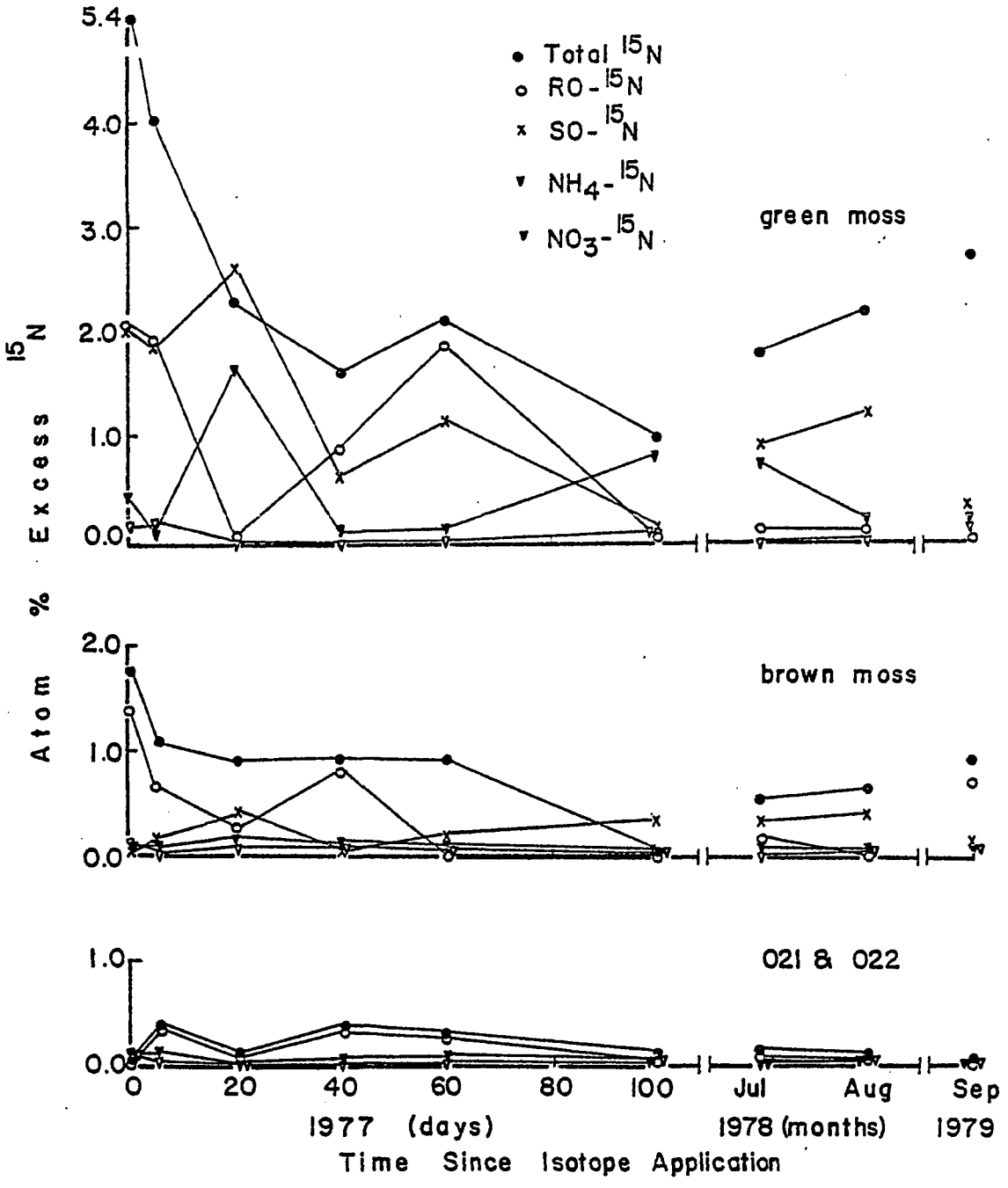

Figure 13. Atom percent excess ^{15}N distribution in selected pools of forest floor on the permafrost-dominated site (100% $^{15}NH_4Cl$ application)

as the total N label continued to decline until 20 days after application. Between 20 and 40 days SO-N and NH_4-N label dropped in conjunction with an increase of isotope in the recalcitrant RO-N pool. From 40 to 60 days the label reappears more strongly in total and RO-N pools, while atom % excess ^{15}N in the more available forms, such as SO-N, NH_4-N, and NO_3-N, stays low. At the end of the first growing season (100 days) almost equal amounts of isotope occurred in the total and NH_4-N pools. The remaining N pools showed little enrichment at that point. During the second year of the experiment total N persisted as the dominant form of N tying up the isotope, although ^{15}N was still present at fairly high levels in the NH_4-N pools in July 1978 and SO-N pool in July and August 1978. At the end of the third growing season ^{15}N is tied up largely in the unavailable form at the expense of available N pools, a pattern that was consistent at both black spruce sites for all treatments and forest floor components.

The brown moss layer on the $^{15}NH_4Cl$ treatment at Washington Creek showed fewer and more damped oscillations in isotope ratios of the N pools examined, suggesting fewer instances of nitrogen transfer (movement from one pool to another) occurring at a lower rate compared to the green moss layer above. This could be ascribed to reduced temperatures in this layer compared to the moss surface, with a concomitant reduction in microbially mediated nitrogen mineralization/immobilization processes. The lower atom % excess ^{15}N values encountered in this layer could be further indication of a filtering action on the

part of the living moss tissue.

Lowest isotope enrichment occurred in the combined 021+022 layer. The fairly large natural SO-N pool present in this layer (cf. Table 4 and 6) was not labelled at all and the NH_4-N and NO_3-N pools showed very low enrichment, not exceeding 0.1 atom % excess ^{15}N. Most of the ^{15}N that could be detected was contained in the total and RO-N pools and movement between these unavailable and the more available pools of N appears to having been kept at a minimum, indicating that nitrogen immobilization is the dominant process in this forest floor layer.

On the $K^{15}NO_3$ treated plot at Washington Creek similar relationships between forest floor layers and nitrogen pools could be observed (Fig. 14). In the green and brown moss layers the SO-N pool became labelled early in the first growing season and at 20 days after application showed highest enrichment levels compared to the other forms of N. In the 021+022 layer the SO-N pool remained unlabelled for the duration of the experiment as was the case on the $^{15}NH_4Cl$ treatment. Downward movement of the isotope appeared restricted with nitrogen transfer between N pools being most active in the feather moss layers again emphasizing the importance of the mosses as filtering agents. In the 021+022 compartment total and RO-N were the dominant forms of N with regard to atom % excess ^{15}N throughout the experimental period. In the overlying feather moss layers ^{15}N became tied up in total and RO-N pools at the end of the first growing season and remained largely

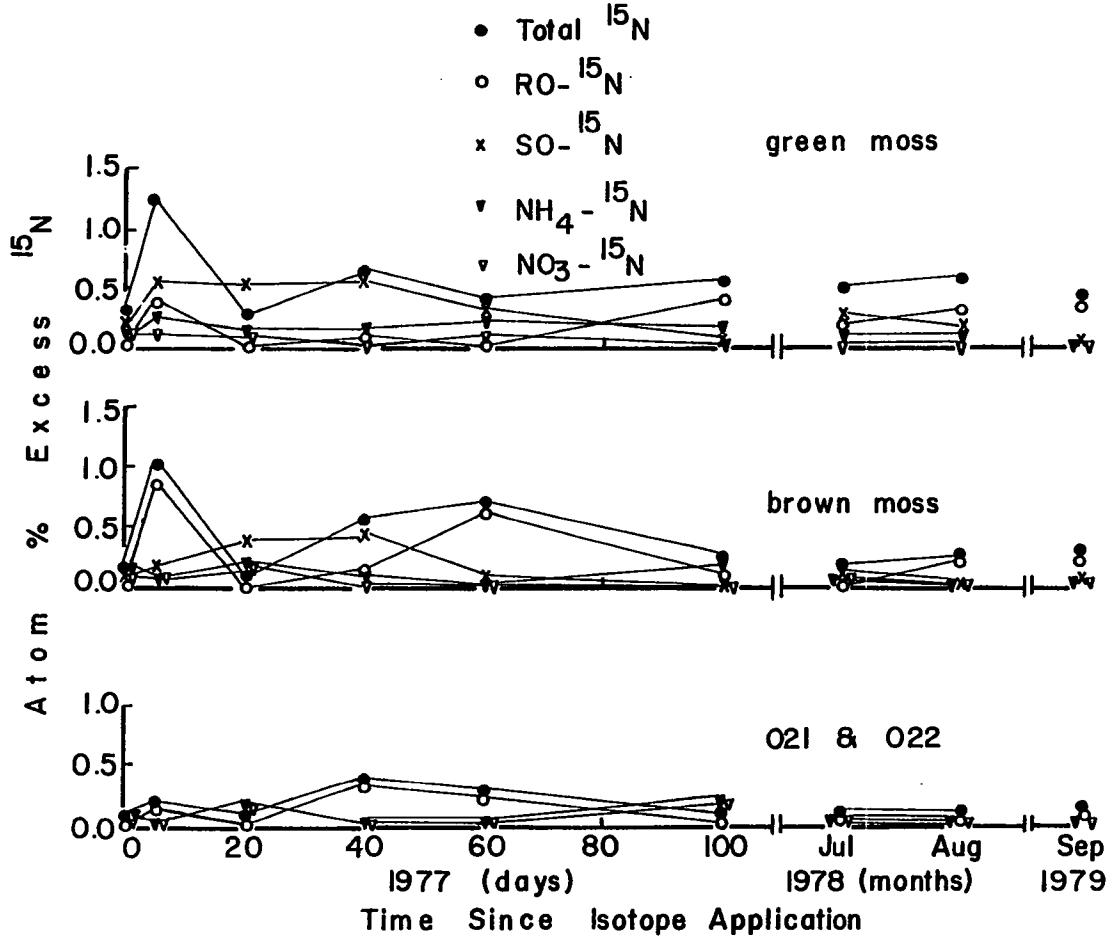

Figure 14. Atom percent excess ^{15}N distribution in selected pools of forest floor components on the permafrost-dominated site (100% $K^{15}NO_3$ application)

there until the end of the third year of sampling. Labelling of the NO_3-N pool was low in all layers reflecting the small natural pool size of this form of nitrogen, low nitrification rates from other pools or rapid flow of small amounts of NO_3-N through this pool. Small atom % excess ^{15}N peaks on the $^{15}NH_4$-N curve at time 60 in the green moss compartment and time 20 in the brown moss, in conjunction with a decrease in total and RO-N ^{15}N pools at this time, would be indicative of low level nitrogen mineralization rates. Significant vascular plant uptake can be largely discounted because of the low enrichment levels in this ecosystem compartment at the end of the third growing season (cf. Table 3). The vascular plant component thus appeared to exert reduced influence over the control of system processes. The problem of leaching will be addressed in the section on selected parameters of soil solution at Washington Creek.

On the $^{15}NH_4Cl$ treated plot of the permafrost-free site at Bonanza Creek (Fig. 15) N dynamics reflected the more favorable physical and chemical regime compared to Washington Creek. After the initial lag in mixing of the isotope with the natural nitrogen pools, discussed earlier, ^{15}N incorporation into the SO-N and NH_4-N pools exceeded that of the total and RO-N pools at 60 days after isotope application in the green moss layer. The high ^{15}N content in the SO-N pool emphasizes forest floor heterogeneity and variability between the two cores used for total and available ^{15}N determination,

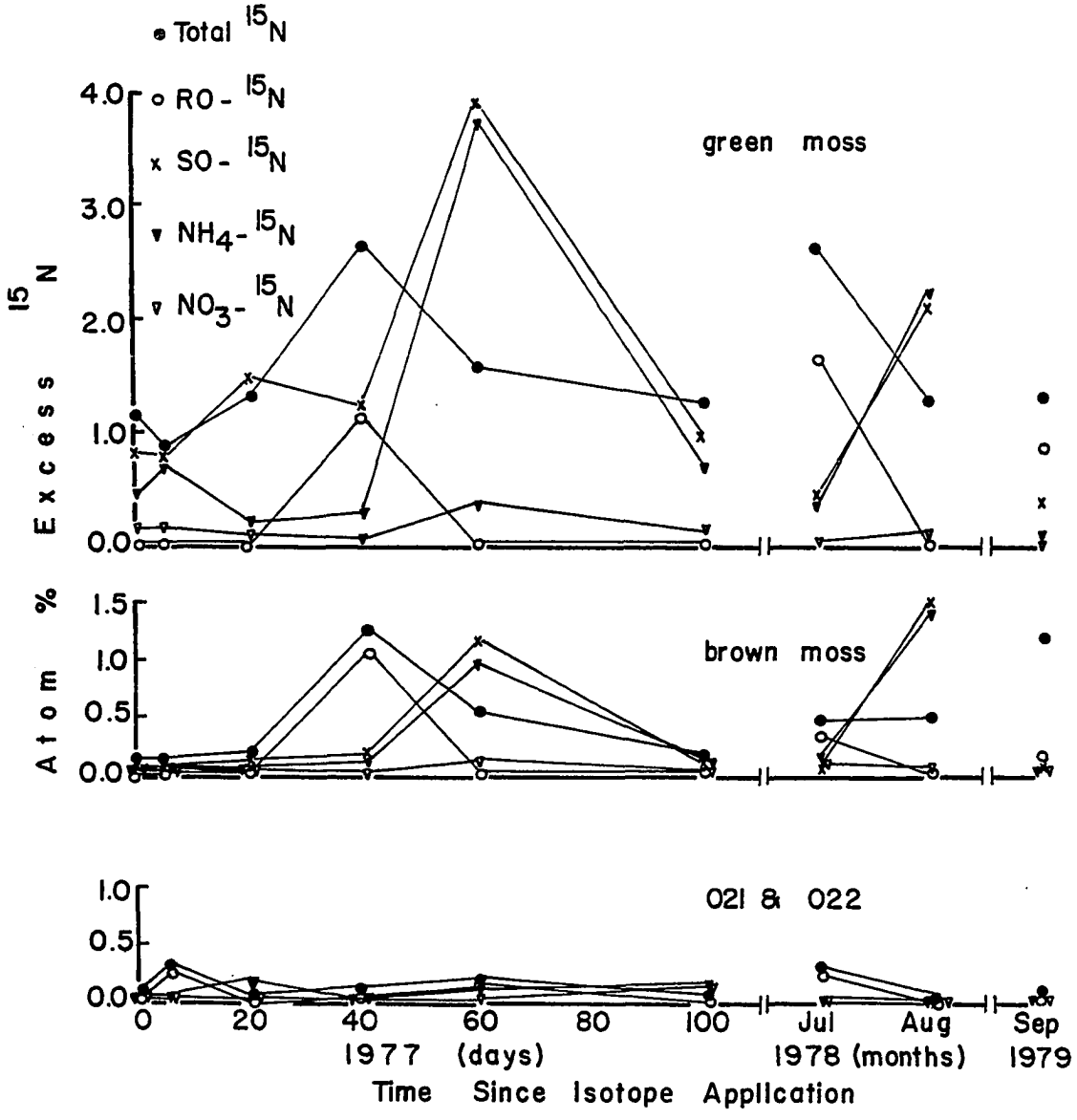

Figure 15. Atom percent excess ^{15}N distribution in selected pools of forest floor components on the permafrost-free site (10% $^{15}NH_4Cl$ application)

respectively, since by definition, the total N pool cannot be exceeded by any other pool. Within 20 days, between time 40 and 60, rapid transfer of the isotope took place from total and RO-N pools. This was followed by renewed immobilization, i.e., incorporation of the isotope into the total N pool and loss from the available pool by the end of the first growing season. During the second year immobilization and mineralization again switched back and forth; initially the isotope appeared predominantly in the unavailable forms and then declined there and became predominant in SO-N and NH_4-N pools. After three years, in September 1979, atom % excess ^{15}N was again highest in total and RO-N fractions while SO-N, NH_4-N, and NO_3-N levels declined to their lowest point. Extension of the experiment into another year would have shown whether immobilization remained the major driving force or if mineralization would have continued to play a role.

Nitrogen dynamics in the brown moss component closely followed that of the green moss with mineralization episodes evident between time 40 and time 60 of the first growing season and again at the end of the second year. Isotope levels at the end of the experimental period were also highest in the unavailable forms RO-N and total N.

In the O21+O22 layer enrichment levels were low, total N and RO-N being the dominant detectable forms of N that were labelled. The SO-N was not labelled and in this respect the two black spruce sites behaved identically. A small peak in the NH_4-N pool at the

end of the first growing season indicates that mineralization proceeded, albeit at a low rate.

The N pools of the $K^{15}NO_3$ treated plot at Bonanza Creek (Fig. 16) were characterized by lower enrichment levels; comparable to the same treatment at Washington Creek. Incorporation of isotopic label from this precursor into unavailable forms of N was rapid in all forest floor layers compared to the NH_4-N treatment. As isotope dilution proceeded total N and RO-N remained the predominantly labelled pools with few exceptions. The occurrence of ^{15}N in readily available forms in excess of unavailable forms was restricted to time 20 and 60 in the green moss layer and time 100 in the brown moss and 021+022 layers. Three years after isotope application the ^{15}N that could still be recovered was almost exclusively tied up in total and RO-N pools of all three forest floor components.

Thus, isotope ratios of selected nitrogen pools alone point out general differences and similarities between the two black spruce sites. N pools of both sites showed high enrichment levels in the moss components whereas the large natural N pools in the 021+022 layer were only slightly labelled suggesting impediment of downward movement of the isotope. The SO-N pool at this depth remained unlabelled throughout the experiment on permafrost-free as well as permafrost-dominated sites, indicating slow turnover (or great age) of total and RO-N pools in the 021+022 layer.

At the end of the experiment nitrogen became tied up in unavailable forms regardless of site, treatment or forest floor component.

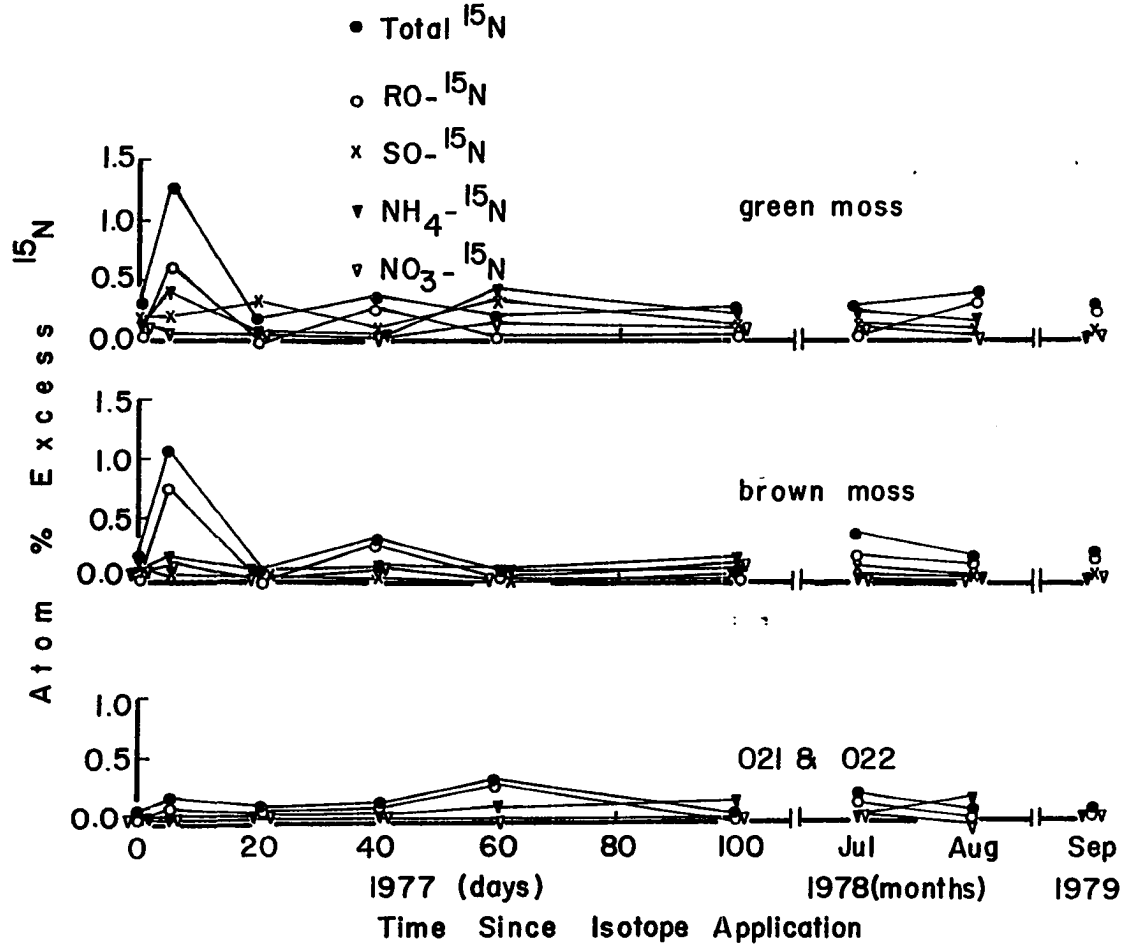

Figure 16. Atom percent excess ^{15}N distribution in selected pools of forest floor components on the permafrost-free site (100% $K^{15}NO_3$ application)

Immobilization/mineralization processes, interpreted from phased increases and decreases in atom % excess ^{15}N of the available vs. unavailable forms, were most pronounced on the $^{15}NH_4Cl$ treated plots of both sites reflecting the dominance of and adaptation to the utilization of ammonium in the system. Higher soil temperatures, manifested by a greater number of degree days at a depth of 10 cm, higher total N content and improved organic matter quality (lower C/N ratios) of the forest floor at Bonanza Creek seemed conducive to more dynamic nitrogen transformation processes in the moss layers at this site compared to Washington Creek. This interpretation would complement findings by Skre and Oechel (1981) who compared seasonal photosynthetic patterns of feather mosses on similar black spruce sites. They concluded that increased soil nutrient content was positively correlated with higher photosynthetic rates in the moss canopy.

Unit weight and unit area determinations

Unit Weight

The great majority of studies that utilize isotopic tracers in ecosystem research extend their treatment of the subject matter beyond discussing atom % excess ^{15}N values alone. An even better understanding can be gained about system properties if isotope ratios are viewed in the larger context of unit weight and unit area expression. Thus, Figs. 17 through 20 show the amount of ^{15}N contained in a gram of forest floor layer for the N pools examined on the two black spruce

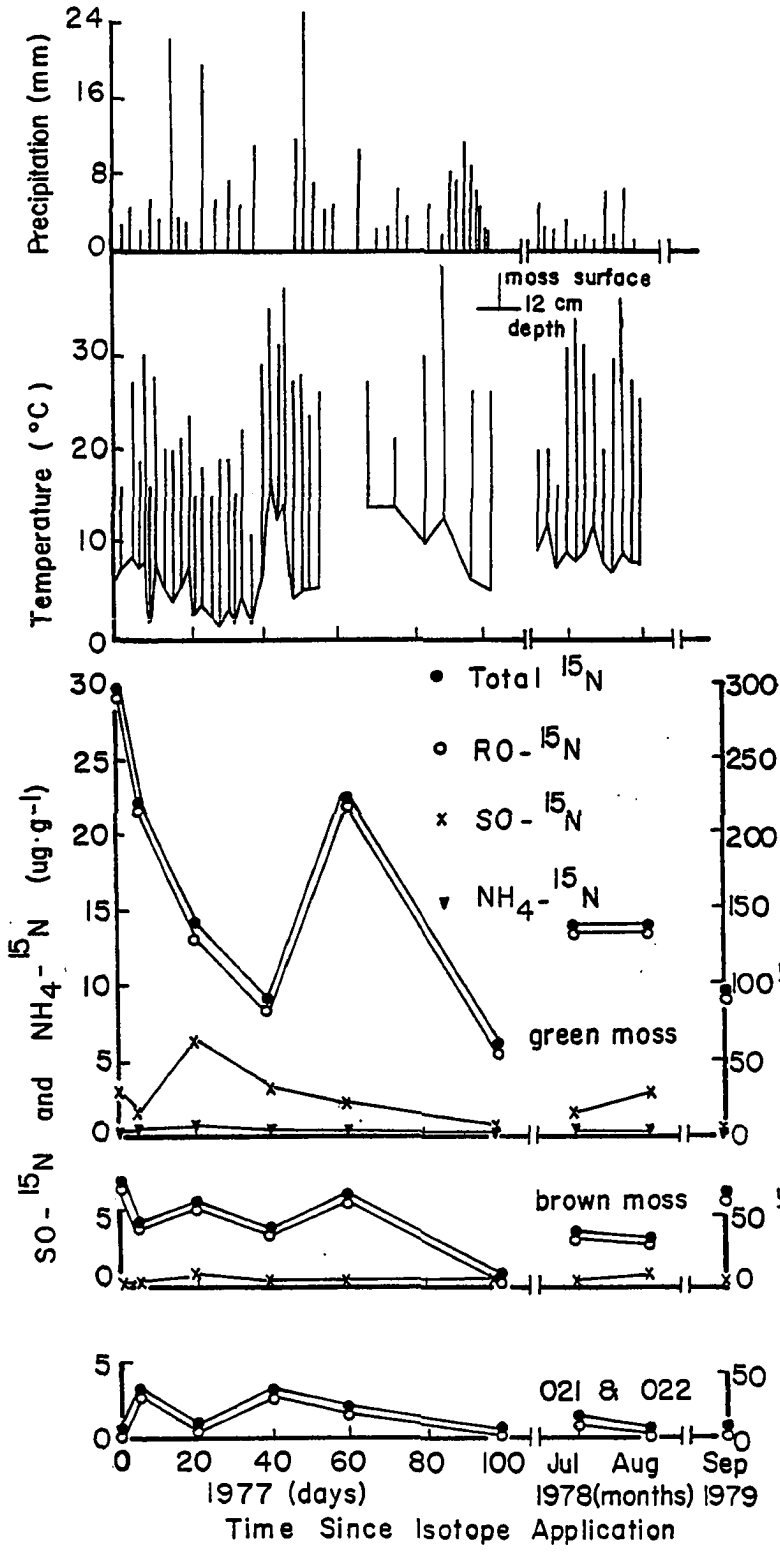

Figure 17. ^{15}N distribution (ug·g^{-1}) in selected pools of forest floor components on the permafrost-dominated site (100% $^{15}NH_4Cl$ application) and seasonal temperature and precipitation patterns

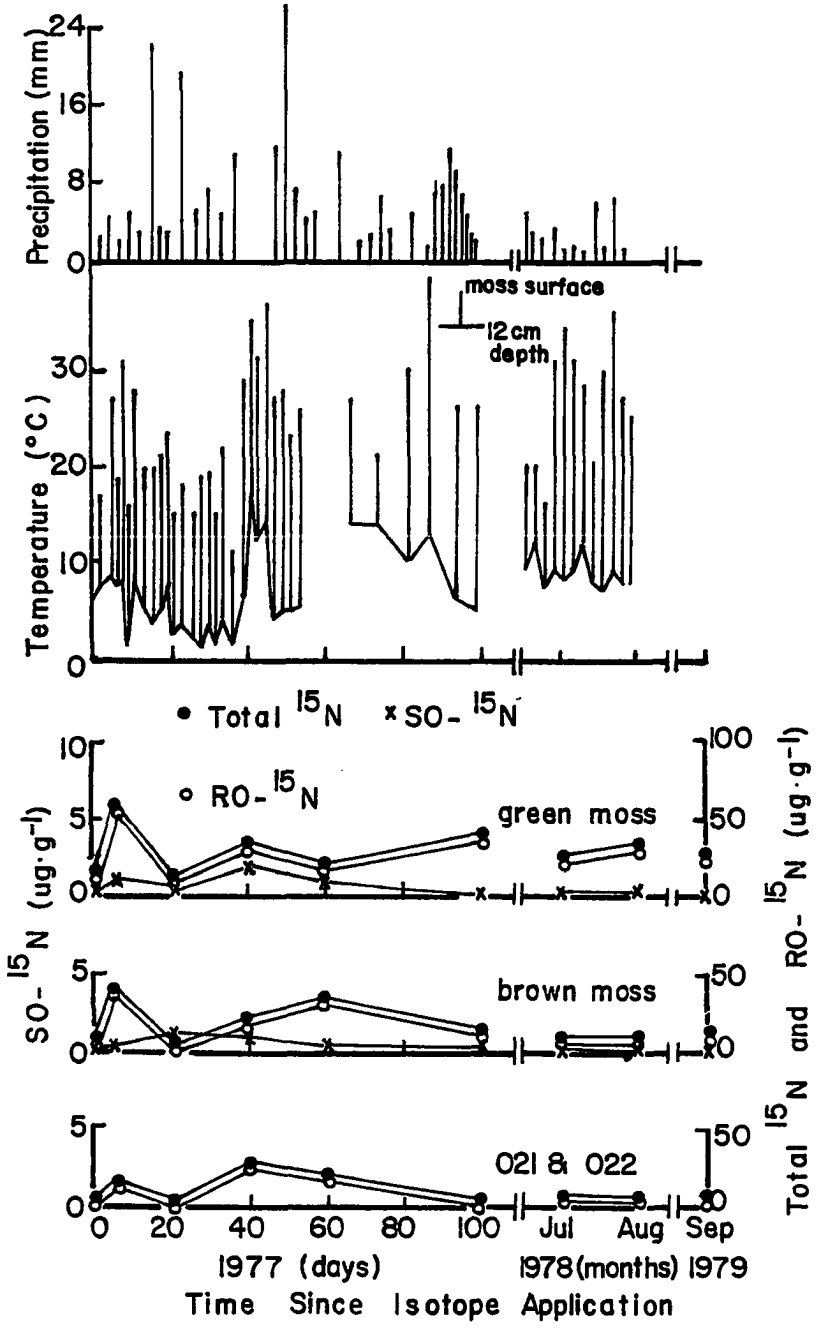

Figure 18. ^{15}N distribution ($ug \cdot g^{-1}$) in selected pools of forest floor components on the permafrost-dominated site (100% $K^{15}NO_3$ application) and seasonal temperature and precipitation patterns

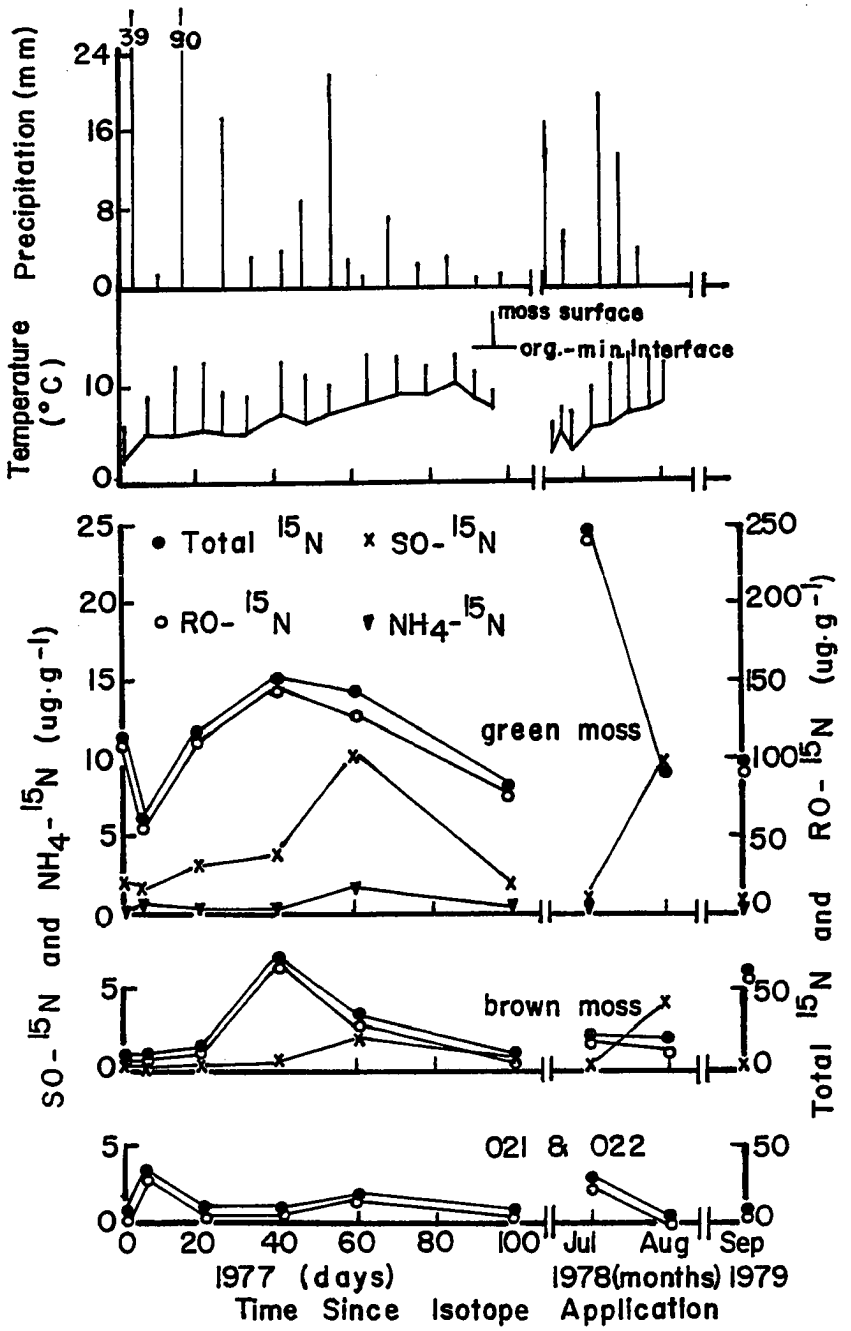

Figure 19. ^{15} distribution (ug·g^{-1}) in selected pools of forest floor components on the permafrost-free site (10% $^{15}NH_4Cl$ application) and seasonal temperature and precipitation patterns

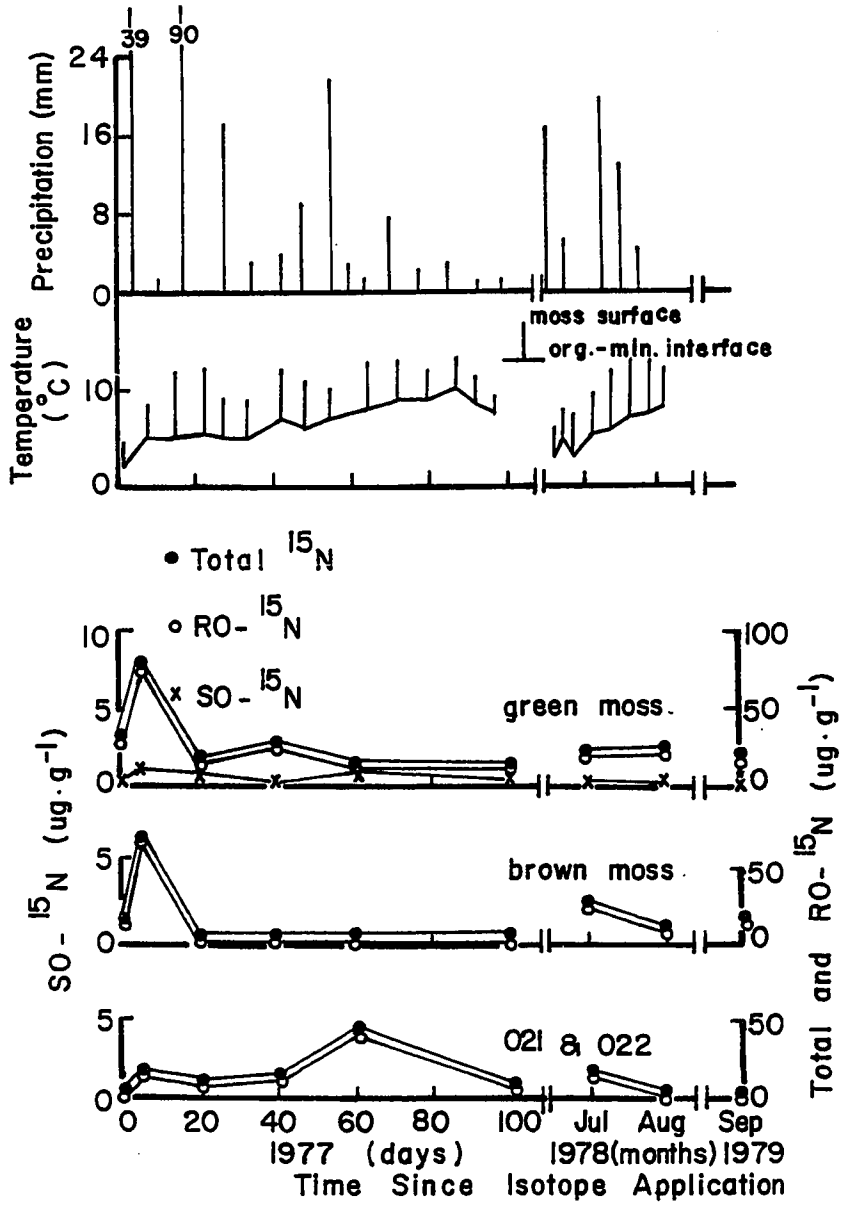

Figure 20. ^{15}N distribution ($ug \cdot g^{-1}$) in selected pools of forest floor components on the permafrost-free site (100% $K^{15}NO_3$ application) and seasonal temperature and precipitation patterns

sites. It will be noted that $^{15}NH_4$-N pool dynamics are only shown for green moss layers of the $^{15}NH_4Cl$ treatments (Figs. 17 and 19) and that $^{15}NO_3$-N pool sizes are not shown at all (Figs. 17 through 20). When omitted, $^{15}NH_4$-N and $^{15}NO_3$-N pool sizes never exceeded 0.20 and 0.07 $ug \cdot g^{-1}$, respectively. Climatic data (precipitation and forest floor temperature) are included here since moss and substrate nitrogen cycling processes have previously been linked, with varying degrees of success, in a wide array of environments, to seasonal climatic fluctuations (e.g. Belser, 1979; Dilks and Proctor, 1976a, 1976b; Flanagan and Van Cleve, 1977; Kowalenko, 1978; Loftis and Kurtz, 1980; Pitkin, 1975; Tallis, 1959; Witty, 1979).

On the $^{15}NH_4Cl$ treated plot at Washington Creek total and RO-^{15}N were the dominant forms of nitrogen with the green moss containing the largest pool sizes (Fig. 17). NO_3-^{15}N pools were small in all three layers, never exceeding 0.07 $ug \cdot g^{-1}$ of layer. The SO-^{15}N pool which is prominent in green and brown moss layers, is absent in the 021+022 layer because of the failure of the tracer to be incorporated in this pool on all treatments of both sites indicating low levels of mineralization. In the green moss layer the SO-^{15}N pool increased to its highest level 20 days after initiation of the experiment as total and RO-^{15}N levels declined. Since $^{15}NH_4$-N and $^{15}NO_3$-N pools remained low during this period it would follow that the peak in the SO-^{15}N pool at time 20 was a result of movement of ^{15}N from total and RO-^{15}N pools into this more soluble

form of N. The mechanism accounting for this movement could be related to ^{15}N mineralization, some hydrolytic activity or leaching of low molecular weight organic ^{15}N. It also indicates that the initial decline in total and RO-^{15}N pools is not only a function of simple isotope dilution, but also reflects isotope movement out of these pools into the more available SO-^{15}N pool. After time 20 and up to time 40 all nitrogen pools declined in the green moss layer. Between time 40 and time 60 there was a sharp rise in the organic ^{15}N pools as the SO-^{15}N pool continued to decrease. Within the 20 days that lead up to the total and RO-^{15}N peaks climatic conditions were extreme. For approximately 8 days after the time 40 sampling forest floor temperatures showed record highs while no precipitation was recorded. That period was followed by drastically lowered substrate temperatures while record rainfall was recorded around time 50. From then on towards time 60 forest floor temperature again started to climb and precipitation events were reduced to shower activity. The build-up in total and RO-^{15}N pools of this layer during the sampling interval was not compensated for by an equivalent decline in the available pools. One explanation for this would be the uneven mixing of label with forest flow layers. It is also possible that during periods of desiccation, when photosynthesis is inhibited by moisture stress (Skre and Oechel, 1981) nutrient assimilation and transformations are similarly affected, slowing down the isotope dilution trend

and affecting tissue isotope ratios in such a way that an apparent increase in total and RO-^{15}N pools is recorded. With the resumption of physiological activity during a wetting cycle accelerated isotope dilution through synthesis of new tissue may result in a decrease in the unavailable pools without a concomitant increase in the available pools as was the case between time 60 and the end of the growing season (time 100).

Since nutrient uptake by the feather mosses from the substrate is rather limited, and only occurs by capillary action when a continuous water film is established between the moss tufts and the substrate (Anderson and Bourdeau, 1955; Mägdefrau, 1977; Tallis, 1959) moss growth and nutrient assimilation are not subject to rigid internally-imposed patterns. Instead, the availability of water is of overriding importance. For example, Pitkin (1975), studying growth patterns in corticolous pleurocarpous mosses in England, determined that vegetative elongation growth was largely dependent on the periodicity and duration of wetting conditions. This was confirmed by Bates (1979), Longton and Greene (1979) and Skre and Oechel (1981) for Pleurozium schreberi. Temperature may act as a secondary controlling factor, low temperatures in the fall and early spring inhibiting growth when plant water contents are otherwise optimal (Bates, 1979). Moisture has also been identified as a major controlling factor for nitrogen fixation by blue-

green algae association with the feather moss canopy in interior Alaska black spruce forests (Billington and Alexander, 1978). Using ^{15}N as a tracer, the nitrogen fixed by algae has been shown to follow the upward movement of water along the plant stem in the case of Sphagnum in northern Sweden. Enrichment of plant tops from labelled substrate occurred within two hours after application (Basilier, 1980). Although the rate of nitrogen fixation (acetylene reduction) by blue-green algae is generally considered to be low ([less than 1 $nmol \cdot g^{-1} \cdot h^{-1}$] Billington and Alexander, 1978; Basilier, 1979) it may have been a contributing factor in the observed decline after time 60. Witty (1979) studying algal nitrogen fixation on temperate arable fields determined that fixation markedly increased after a two-week period of relatively heavy rainfall (in excess of 10 mm), but was unresponsive to high soil temperatures (15°C). The species involved in nitrogen fixation were Nostoc spp. and Anabaena sp., of which the former has been implicated in nitrogen fixation in epiphytic association with Sphagnum in coniferous forests of sub-arctic Scandinavia (Basilier, 1979; 1980; Granhall and Lindberg, 1978).

Bellamy and Rieley (1967) contended that any ions rising with the capillary water along the moss stem are either fixed at exchange sites, presumably unesterified polyuronic acids in the cell walls (Clymo, 1963), or that rain falling on the moss canopy continuously leaches the ions back into deeper layers. The latter scenario

suggests that the green moss layer should become enriched with and depleted of ^{15}N in response to drying and wetting cycles, respectively, surface evaporation being the driving force for capillary water movement. It is difficult to ascertain whether the present data bears this out since the above authors did not specify the threshold of moisture content that would trigger either downward movement or upward capillary rise of water containing the isotope. On the other hand, Molchanova and Bochenina (1980) studying Hylocomium splendens and Pleurozium schreberi as accumulators of radionuclides found that the strategy of these species to grow in dense "carpets" promotes long-time retention of aqueous solutions. This results in enrichment of the mosses over time as radioactive substances arrive with precipitation and surface runoff, a situation somewhat analogous to the filtering action of exchange resins, through high surface exchange capacity. The authors concluded that together with the slow growth and atrophy of mossy vegetation and the absence of shedding in it, the rate of nuclide excretion is very low under natural conditions. If the principle can be applied to such stable isotopes as ^{15}N it would account for the observed persistence of ^{15}N in the moss layers since at the end of the third growing season over 95% of the total and RO-^{15}N was contained in green and brown moss components.

Superimposed over seasonal variations in ^{15}N content in the moss layer due to climatic events or periods favorable for N fixation are periodic spurts in dry matter production of the mosses which would show up on the graph as accelerated isotope dilution. In order to separate this latter effect from simple physical isotope movement or biological N fixation, seasonal moss production measurements would be required.

The brown moss layer on the $^{15}NH_4Cl$ treatment at Washington Creek showed less pronounced fluctuations in the smaller (compared to green moss) total and RO-^{15}N pool sizes (Fig. 17). With increasing depth from the green moss surface, temperature and moisture conditions can be expected to be more stable and fluctuations in biological activity associated with N transformations to be damped. This is reflected in reduced oscillations in nitrogen pool size. The dip in total and RO-^{15}N pool sizes at the end of the first growing season is somewhat puzzling since movement into the SO-^{15}N at that time did not fully account for the decrease. Leaching into the O21+O22 layer can be excluded as an explanation since no increase could be detected there, but leaching out of the system entirely and/or uptake and removal by trees cannot be discounted as a possibility. The previously mentioned dilution in pool size due to a production spurt can also be discounted since this part of the moss plant is not involved in dry matter production any more. It is possible

that some of the isotope moved upward in response to drying conditions prevalent prior to this sampling day.

In 021+022 layers ^{15}N is tied up virtually completely in total and RO-^{15}N pools. Damped oscillation peaks and troughs in pool size during the first growing season were mirror images of fluctuations in the brown moss layer above, indicating that some physical movement between the two compartments must have taken place. No mineralization was evident or what mineralization had taken place was associated with rapid removal of its products.

Since the brown moss layer had higher $^{C}/N$ ratios than the combined 021+022 layer (83 vs. 63, respectively), it could be expected that, from this standpoint, decomposition rates and return of available forms of N to the forest floor would be greatest in the 021+022 layer. The fact that this was not the case, indicated by permanently very small $^{15}NH_4$-N and $^{15}NO_3$-N pool sizes and failure of the SO-^{15}N pool to exhibit any activity, suggests that low temperature at this depth was the controlling factor in nitrogen transformations rather than substrate quality.

^{15}N pool sizes on the $K^{15}NO_3$ treated plot at Washington Creek were lower in green and brown moss compartments, but comparable to the $^{15}NH_4Cl$ treated plot in the 021+022 layer (Fig. 18). All forest floor components had small $^{15}NH_4$-N and $^{15}NO_3$-N pool sizes, not exceeding 0.01 $ug \cdot g^{-1}$ of layer. The SO-^{15}N pool showed peak maxima

of 1.2 and 0.7 $\mu g \cdot g^{-1}$ in green and brown moss layers, respectively. After initial immobilization of $^{15}NO_3$-N in total and RO-^{15}N pools their size was subject to only small amounts of fluctuations for the duration of the experiment. The peak in total and RO-^{15}N pool sizes in the O21+O22 layer at time 40 would indicate downward movement of the isotope. This translocation seemed to have been related to precipitation events as there was frequent rainfall prior to that sampling date. Since there was no accumulation of $^{15}NO_3$-N at this depth the isotope must have moved in organic form, was quickly immobilized in this compartment to organic N or leached beyond this zone. Organic forms of nitrogen that would be involved were probably protein complexes or other low molecular weight compounds such as amino acids and amino sugars. Greenfield (1979) presented evidence that the bulk of soil organic N occurs in this form.

It should be emphasized at this point that the ^{15}N pool sizes measured are not wholly attributable to plant nitrogen. Nitrogen incorporated in live and dead microbial and invertebrate tissue was not distinguished from that of live and dead plant material since no attempt was made to measure microbial nitrogen separately from live and decomposed plant material. Consequently, the organic ^{15}N recovered in brown moss and O21+O22 layers does not solely represent structural nitrogen formerly in the green compartment. It may partially represent N mineralized from decomposing plant material and subsequently immobilized in microbial tissue.

^{15}N dynamics involving $^{15}NO_3$-N as the precursor pool has again been shown to be sluggish compared to $^{15}NH_4$-N. Nitrogen transformations involving NO_3-N, such as nitrification and ammonification appeared to have taken place at low rates. The adaptation of the system as a whole to the dominance of ammonium seemed to have curtailed nitrogen transformations with $^{15}NO_3$-N as an intermediate or terminal product. However, besides rapid loss from the system as a whole, it could also be argued that NO_3-N is such a "rare and prized commodity" that its accumulation in the system for any length of time was prevented by immediate plant and microbial uptake and conversion to organic forms of N, i.e., the rapid-flux scenario offers itself again as a possible explanation.

The $^{15}NH_4Cl$ treatment of the permafrost-free site at Bonanza Creek reflected the more favorable thermal and substrate quality regime of the site compared to Washington Creek (Fig. 19). Nitrogen in the SO-^{15}N pool played a more pronounced role in green and brown moss components. ^{15}N in total and RO-^{15}N pools appeared to have been shifted physically from the green through brown into the O21+O22 compartment within 5 days after application of the tracer as indicated by the decline of these pools in the green moss and their increase in the O21+O22 layer. Heavy precipitation on the day before sampling could have been responsible for the observed shift in pools. Between 5 and 40 days after the beginning of the experiment organic pool sizes in the O21+O22 layer decreased in

conjunction with increases of organic pool sizes (including SO-^{15}N) in green and brown moss. The decrease in O21+O22 did not account fully for all of the increase in the forest floor layers above, again pointing to the problem of instantaneous and homogeneous mixing of label with the medium to which it was applied.

It should be recalled at this point that the $^{15}NH_4Cl$ application at Bonanza Creek was only at 10% of the available pool size compared to 100% at Washington Creek. The reason that atom % excess ^{15}N and hence ug $^{15}N \cdot g^{-1}$ values at Bonanza Creek fell within the range of Washington Creek data is related to the large natural NH_4-N pool size at Bonanza Creek which required that the 10% $^{15}NH_4Cl$ dose be almost as large as the 100% $^{15}NH_4Cl$ dose at Washington Creek (cf. Table 3). One question that arises and is presently unanswered addresses the problem of concentration dependence of reaction rates, i.e., was there a more rapid dilution and movement of the isotope through the forest floor at Bonanza Creek as compared to Washington Creek since the application rate was only equivalent to 10% of the NH_4-N pool size? This question can be extended to include reaction kinetics on $K^{15}NO_3$ vs. $^{15}NH_4Cl$ treated plots since the former received a much smaller application of ^{15}N than the latter. An experimental design resembling the study of enzyme kinetics whereby reaction velocity is related to substrate concentration might be a useful approach to resolve this problem.

Between time 40 and time 60 there was a dramatic increase in the

SO-^{15}N pool of green moss layer and to lesser extent in the $^{15}NH_4$-N pool. The SO-^{15}N pool of the brown moss similarly showed an increase while its $^{15}NH_4$-N was not affected by any mineralization of total or RO-^{15}N. ^{15}N pools of the 021+022 layer were unaffected by the nitrogen transformation occurring above indicating little vertical transformation of ^{15}N. The precipitation pattern during this active period of shifting pool sizes was characterized by frequent rains of increasing magnitude. The apparent response to this wetting cycle was mobilization of nitrogen from unavailable to more readily available forms, indicating that conditions prior to this were not as conducive to microbial mineralization processes. Nitrogen fixation has also been shown to be affected by rainfall patterns. Loftis and Kurtz (1980), examining N added to soil by rainfall and blue-green algae in west Texas determined that frequent showers caused N fixing organisms to be more active than when the same amount of rainfall occurred at one time.

After time 60, up to the end of the growing season, a drying cycle prevailed which apparently was unfavorable for further mineralization episodes. In the green moss layer SO-^{15}N and $^{15}NH_4$-N pool sizes decreased and ^{15}N was again shifted to the more recalcitrant RO-^{15}N pool, while brown moss pool sizes decreased slightly; little or no activity could be detected in the 021+022 component. From this discussion it emerges that the scenario proposed by Bellamy and Rieley (1967), whereby water and nutrients contained

therein are leached to lower layers in response to wetting conditions, does not fully explain the mechanism of ^{15}N dynamics in the forest floor of black spruce ecosystems. In the present study the wetting cycle did not appear to have flushed nitrogen into lower layers. Instead it triggered release of ^{15}N from the unavailable to available forms which remained in the green moss layer.

In July 1978, after the first overwintering season, almost all of the ^{15}N in the moss layers was tied up in total and RO-^{15}N pools. There was also a peak in organic ^{15}N pools of the O2l+O22 layer at this time, reflecting some downward movement of ^{15}N during the sampling interval. Between July and August of 1978 another burst in nitrogen mobilization had taken place in the green moss layer. The ^{15}N liberated appeared in the SO-^{15}N pools of all forest floor layers in August 1978 at a time when forest floor temperatures were on the increase as precipitation activity decreased. By the end of the experiment, in September 1979, nitrogen had again become tied up in total and RO-^{15}N pools of all forest floor layers. It would probably require the monitoring of subsequent seasonal trends in order to determine with certainty whether tying up of ^{15}N in unavailable form prior to the onset of winter is a consistent pattern reflecting nitrogen conservation in the system.

The $^{C}/N$ ratio relationships in the forest floor are similar to the situation at Washington Creek, being lower in the O2l+O22 than

in the brown moss layer above indicating that temperature controls rather than substrate quality appeared to have been the crucial factor in determining decomposition and nutrient transformation processes there.

From weekly temperature measurements taken at the forest floor surface and organic/mineral soil interface some insight can be gained into the effect of temperature on forest floor nitrogen mineralization/immobilization reactions. After the steady rise of the temperature curve during the summer there was an eventual decline at the end of the growing season in response to cooler ambient temperature. This decline was associated with tying up of ^{15}N in unavailable pools of the green moss layer, suggesting that temperature may have become limiting to further nitrogen mineralization processes. It would be useful to devise rigorous experimental procedures so that temperature-moisture response surfaces for nitrogen mineralization could be constructed in order to clearly separate the effect of temperature from those of moisture regimes and their respective controlling influence over nitrogen transformations.

The $K^{15}NO_3$ treatment at Bonanza Creek (Fig. 20) showed the now familiar pattern of delayed mixing, small available ^{15}N pool sizes that showed little fluctuation during the three year period and most of the ^{15}N being tied up in total and RO-N. The peak in the 021+022 layer at time 60 occurred at the end of a twenty-day

wetting cycle and reflects downward movement of tagged N. In July 1978 organic ^{15}N had moved up from O21+O22 and reappeared as a small peak in the organic pools of the brown moss layer. At the end of the experiment in September 1979, nitrogen was again sequestered in unavailable pools of all layers.

Unit area

Expression of data on a unit area basis (Figs. 21 through 24) can be used as a check on data interpretation from the previous section which employed unit weight measures. Furthermore, unit area determinations allow the formulation of a balance sheet for recovered ^{15}N since amounts for the original application were calculated in this manner. Soluble organic ^{15}N, NH_4-^{15}N, and NO_3-^{15}N pool dynamics not exceeding 0.6 $mg \cdot m^{-2}$ were omitted from the figures. From Figs. 21 through 24 it becomes immediately clear that the bulk of the isotope is contained in total and RO-^{15}N pools and that the O21+O22 layer is the major storage layer when expressed in terms of $mg \cdot m^{-2}$. Even though atom % excess values were very low in the O21+O22 layer, its great mass, compared to the low density moss layer, makes it the dominant compartment with respect to ^{15}N content. Natural variation in forest floor thickness enters into the calculations and is reflected in the widely varying seasonal ^{15}N content of the O21+O22 layer. It can nevertheless be seen that total and RO-^{15}N pool size variations closely resemble those determined by

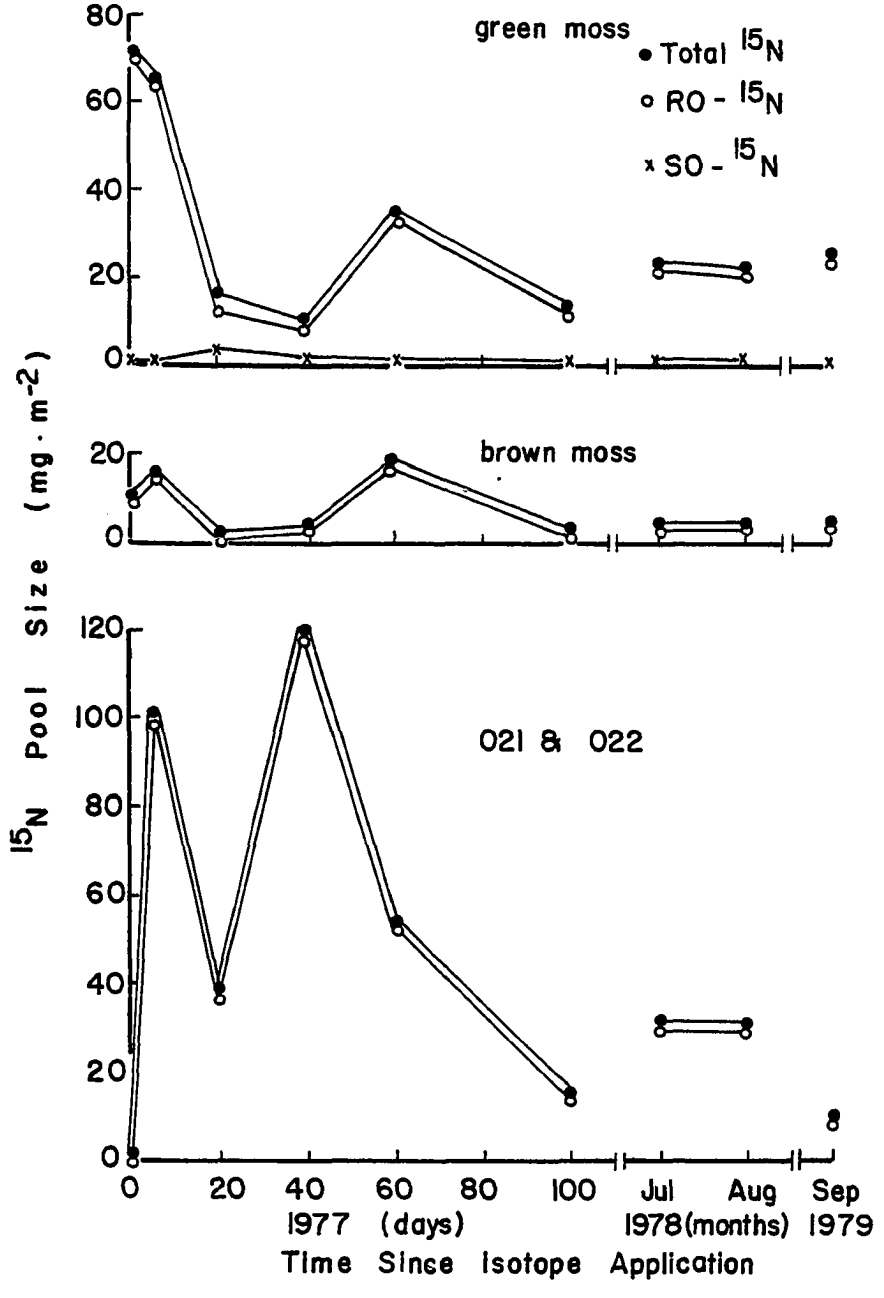

Figure 21. ^{15}N distribution (mg·m^{-2}) in selected pools of forest floor components on the permafrost-dominated site (100% $^{15}NH_4Cl$ application)

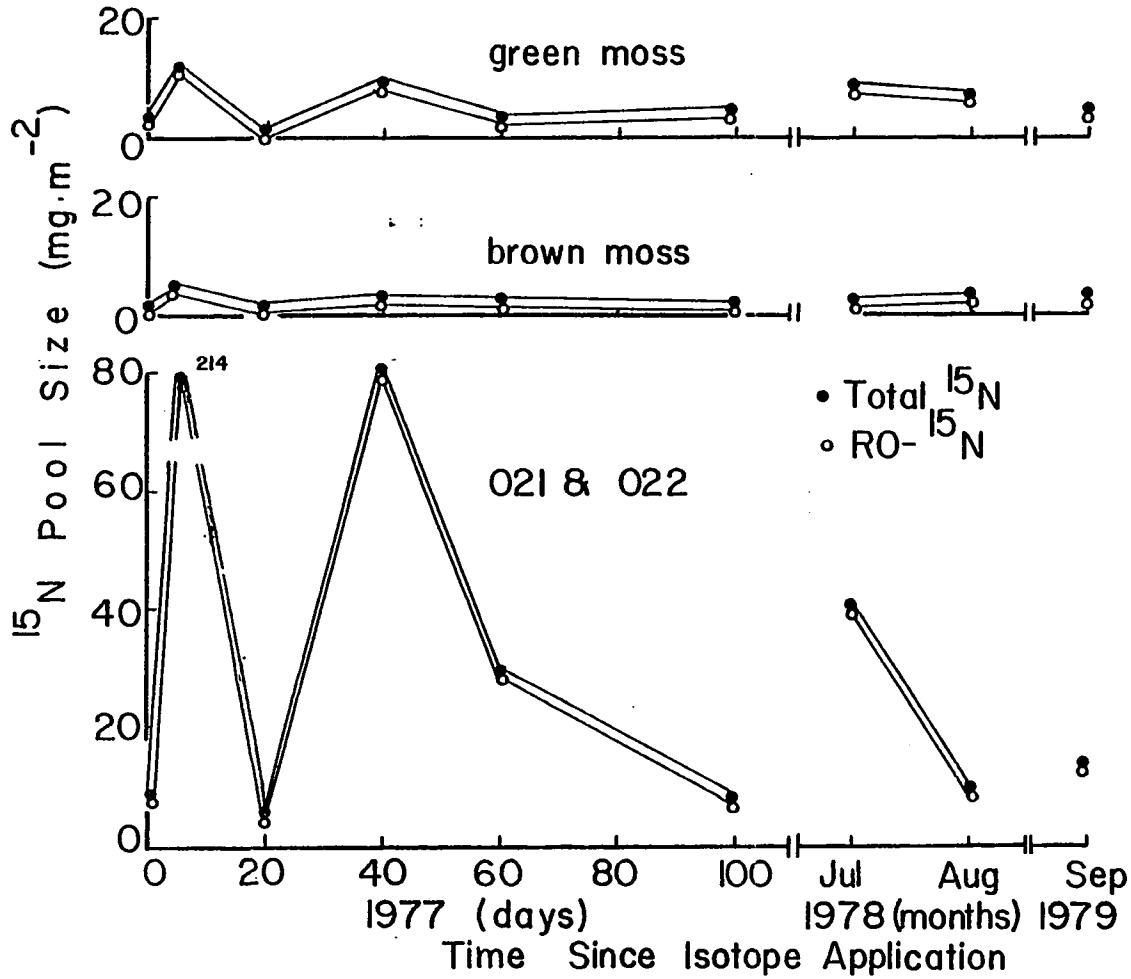

Figure 22. ^{15}N distribution (mg·m^{-2}) in selected pools of forest floor components on the permafrost-dominated site (100% $K^{15}NO_3$) application

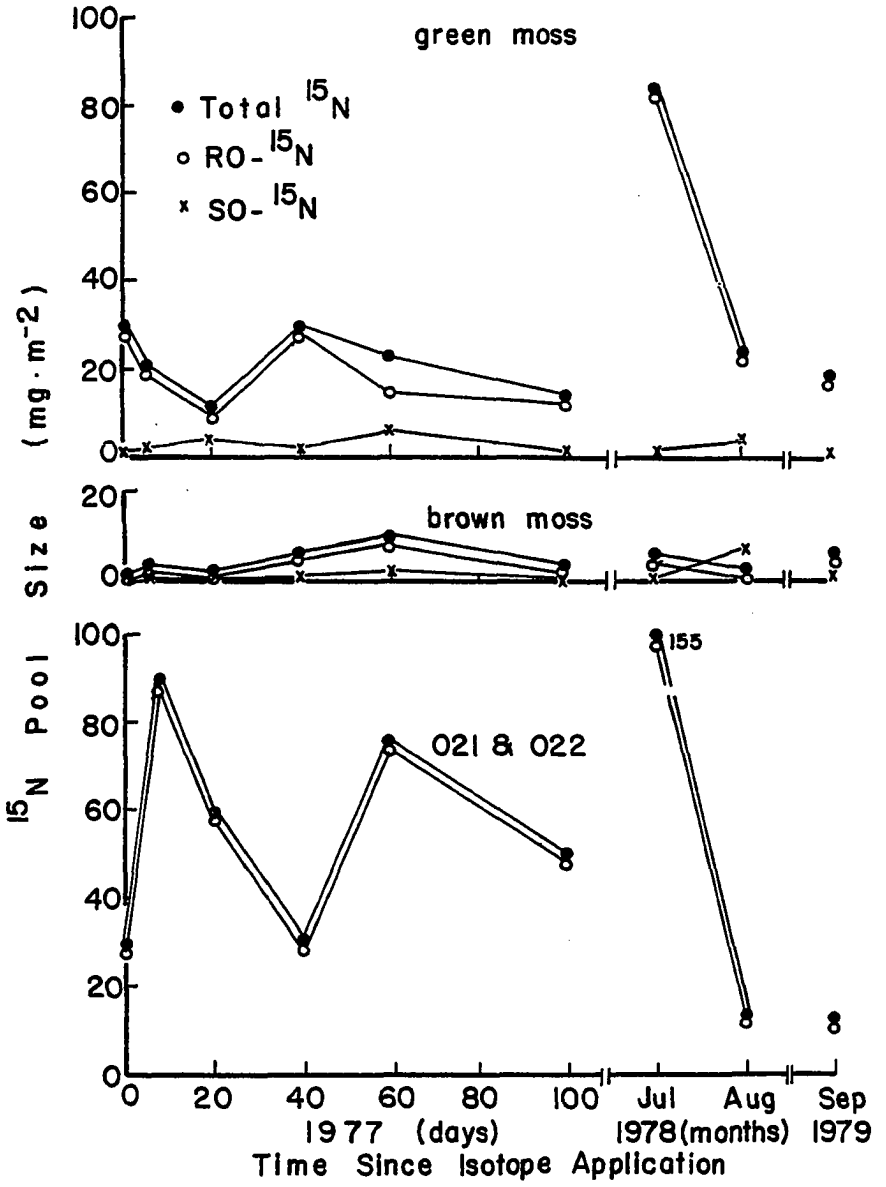

Figure 23. ^{15}N distribution (mg·g^{-2}) in selected pools of forest floor components on the permafrost-free site (10% $^{15}NH_4Cl$ application)

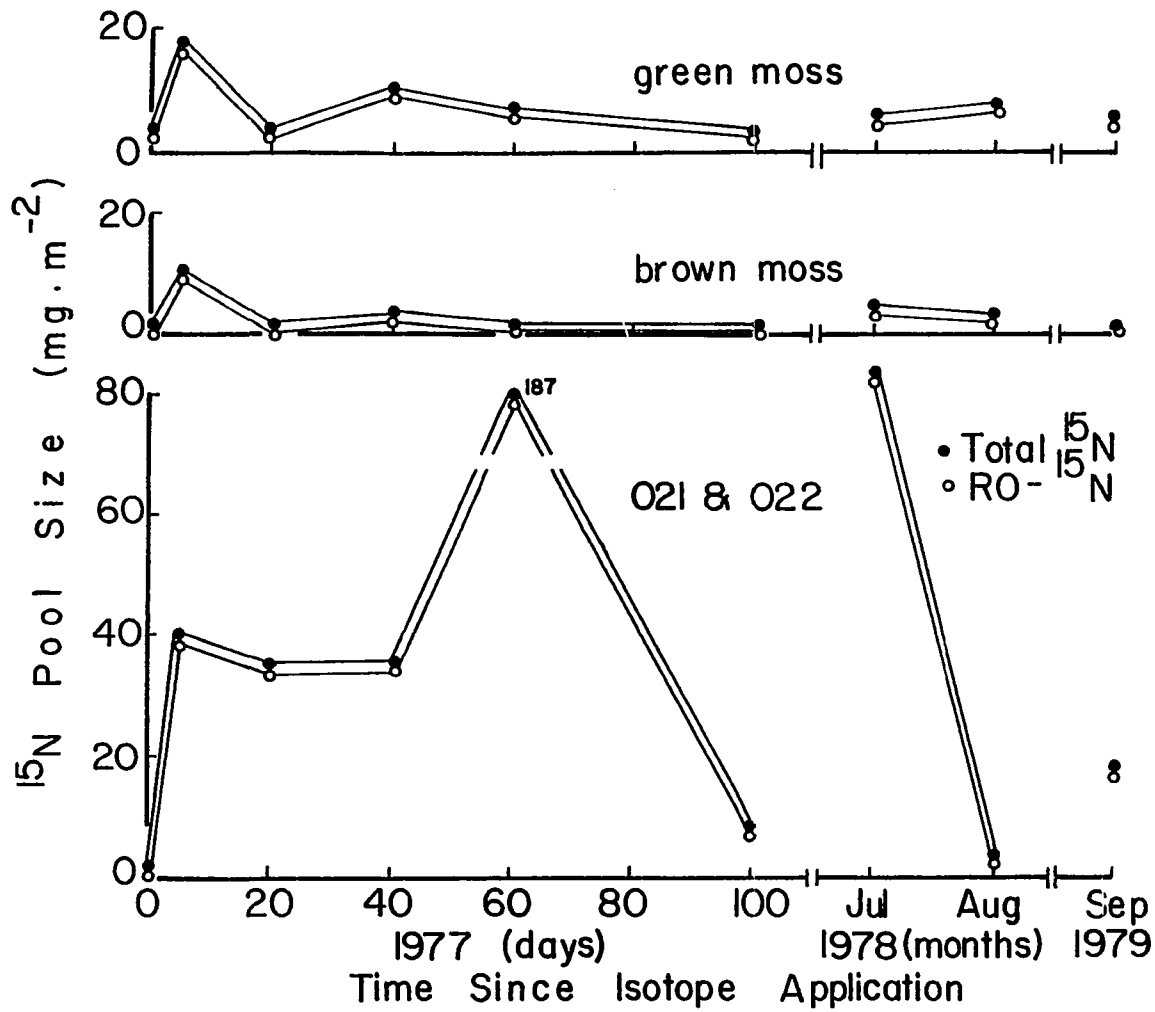

Figure 24. ^{15} distribution (mg·g^{-2}) in selected pools of forest floor components on the permafrost-free site (100% K$^{15}NO_3$ application)

the unit weight method. For example, the peak in total and RO-^{15}N pools of the moss layer on the Washington Creek $^{15}NH_4Cl$ treatment at time 60 (Fig. 21) occurred regardless of method used (cf. Fig. 17). On the Bonanza Creek $^{15}NH_4Cl$ treatment (Fig. 23) the same observation can be made for the July 1978 sampling date (cf. Fig. 19). ^{15}N pools of green and brown moss layers on the $K^{15}NO_3$ treated plots of both sites showed little variation after isotope application which is in agreement with the unit weight method of data presentation (Figs. 22 and 24).

Variations in ^{15}N content of the smaller available pool sizes did not show up as well as when the data was expressed as $ug \cdot g^{-1}$ of layer. This may be considered a lack of sensitivity that makes the unit area method of expression less desirable in this instance. Recent literature dealing with nitrogen mineralization/immobilization processes and employing ^{15}N as a tracer similarly used $ug \cdot g^{-1}$ in their discussion of results (Amato and Ladd, 1980; Ladd and Amato, 1980; Ladd et al., 1977; Sorensen, 1981).

The balance of ^{15}N that could be recovered from the forest floor components for the duration of the experiment is shown in Fig. 25 at Washington Creek and Fig. 26 at Bonanza Creek. Since the original application of ^{15}N was based on previously determined available pool sizes (NH_4-N and NO_3-N) of the combined 021+022 layer and a fixed 021+022 layer depth, forest floor

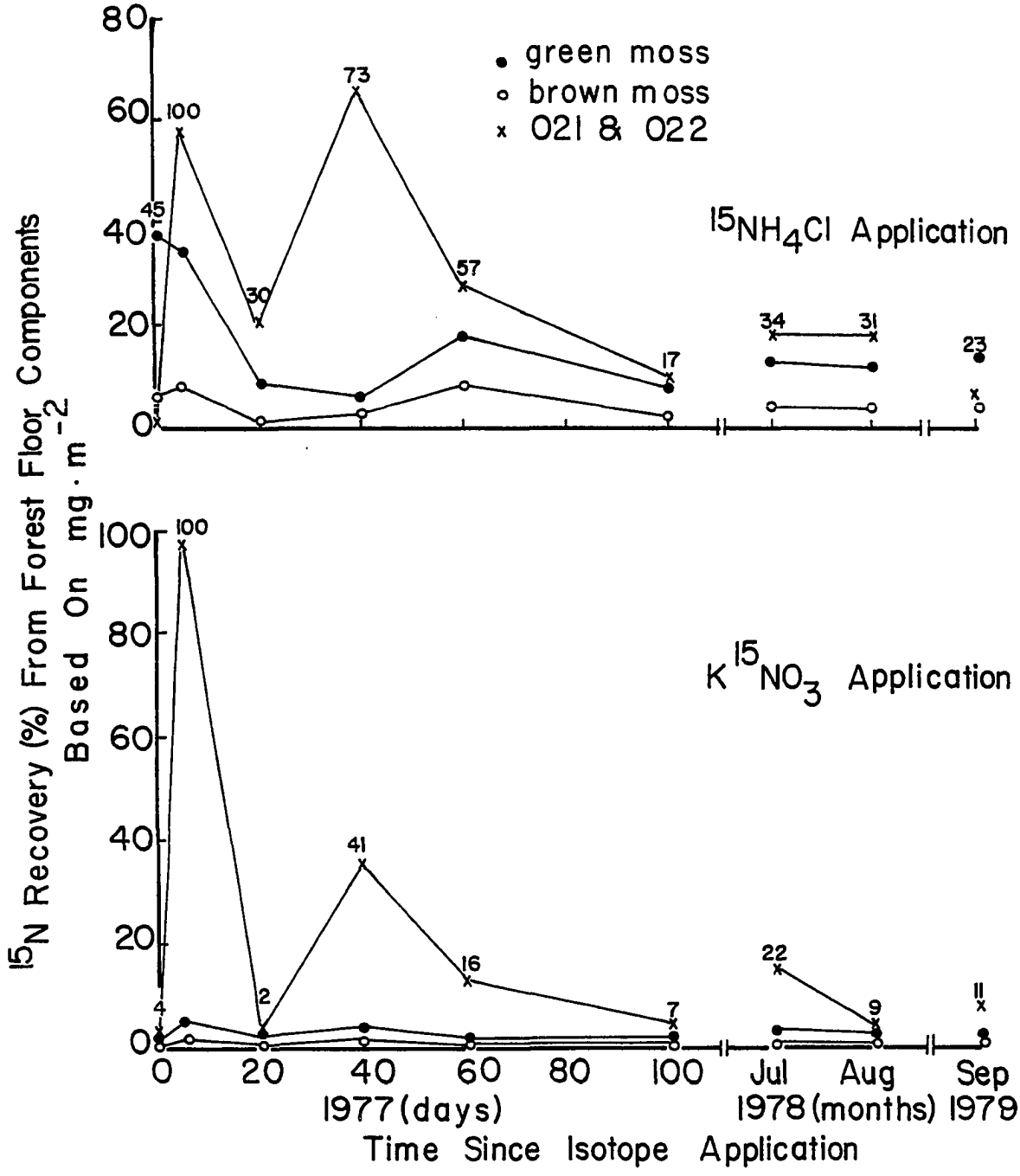

Figure 25. Total forest floor isotope recovery (%) based on mg $^{15}N \cdot m^{-2}$ on the $^{15}NH_4Cl$ and $K^{15}NO_3$ treated plots at the permafrost-dominated site. Values above data points indicate total recovery from all forest floor layers.

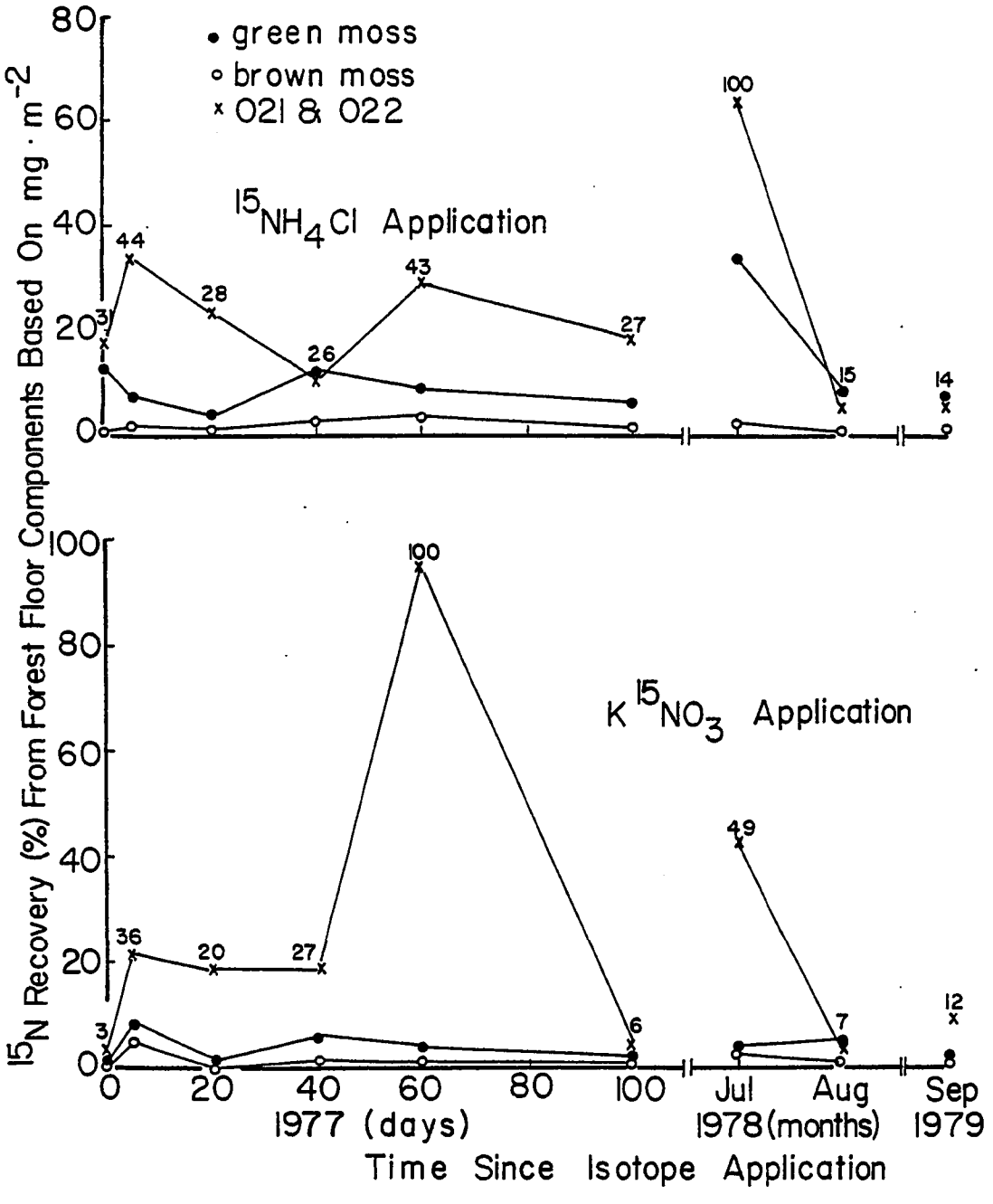

Figure 26. Total forest floor isotope recovery (%) based on mg $^{15}N \cdot m^{-2}$ on $^{15}NH_4Cl$ and $K^{15}NO_3$ treated plots at the permafrost-free site. Values above data points indicate total recovery from all forest floor layers.

variability and uneven penetration of the forest floor by the isotope during the experimental period could show up as ^{15}N recovery in excess of original application. In order to avoid this the highest value for ^{15}N recovered ($mg^{15}N \cdot m^{-2}$) was designated 100% recovery. In the literature that was examined only one instance of ^{15}N recovery in excess of 100% was reported (Legg and Allison, 1967) and without any explanation.

Figure 25 shows percentages of ^{15}N recovered from forest floor components on the two treatments ($^{15}NH_4Cl$ and $K^{15}NO_3$) at Washington Creek. Recovery of ^{15}N was equivalent to 100% on both plots after an initial lag period of 5 days. Subsequently most of the ^{15}N could be recovered from the 021+022 layer until the end of the experiment in September 1979. At that point recovery was higher in the green moss than in 021+022 on the $^{15}NH_4Cl$ treated plot, but not on the $K^{15}NO_3$ treatment, indicating the higher mobility of the anion on one hand and the conservation of the cation on the other. This would be consistent with modern theories of ecosystem strategy whereby the system will conserve potentially limiting materials by concentrating them and withholding them from dilution and loss (Callaghan, 1980; Shaver, 1981; Welsh, 1980). The forest floor compartment responsible for the conservation effort appeared to have been the moss layer in general and the green moss component in particular. Since recovery of available forms of ^{15}N was low in all layers (SO-^{15}N recovery never exceeded 1.8%; $^{15}NH_4$-N and $^{15}NO_3$-N never exceeded 0.4% at Washington Creek and 2.4 and 0.4%,

respectively at Bonanza Creek) nitrogen conservation seemed to have been accomplished by a combination of quick conversion of N from available to unavailable forms (rapid flow through the available pools) and eventual sequestering of these forms in the forest floor. This pattern also held at Bonanza Creek (Fig. 26).

Weetman (1968) and Weetman and Timmer (1967), working in eastern Canadian black spruce ecosystems, proposed that there is a partial interdependence between the vascular plants and the feather mosses that grow beneath them. The vascular overstory provides the shade and the enriched throughfall essential for moss growth. The mosses by their ability to intercept nutrients and dust in precipitation and by their rapid decomposition [sic] provide a source of readily available nutrients to the vascular component which is growing on organic accumulations that decompose very slowly (Weetman, 1968). It should be pointed out that modifications in this scenario can be expected over the wide geographic range of black spruce ecosystems where local climatic influences vary in severity. Thus, decomposition rates and nutrient return by the mosses to vascular plants can be expected to decrease with increase in latitude as was borne out by low enrichment levels in whole plants of the vascular component at the end of the experimental period (cf. Table 3). In addition, as shown by Van Cleve and Alexander (1981), topographic control of system structure and function can be strongly expressed on the local level. Local microclimatic and microtopographic

regimes which in interior Alaska can determine the absence or presence of permafrost, for example, would then superimpose their limitations on the general latitudinal constraints. Evidence for this was provided by the seemingly more dynamic nitrogen transformation processes on the permafrost-free site at Bonanza Creek compared to the permafrost-dominated site at Washington Creek.

Recovery patterns of ^{15}N at Bonanza Creek again bring up the problematic assumption of homogeneous and instantaneous mixing of label in biological systems (Robertson, 1957; Wilde, 1955; Wrenshall, 1955), since 100% recovery of the tracer, to be expected at the onset of the experiment was not accomplished until the second growing season on the $^{15}NH_4Cl$ treated plot and until 60 days after application on the $K^{15}NO_3$ treatment (Fig. 26). It becomes apparent that the surface applied isotope penetrated the forest floor unevenly, resulting in pockets that may have been more highly enriched than immediately adjacent areas. Forest floor inhomogeneities would cause this non-uniform distribution, where old root channels or dead roots for example, could act as rapid conduit or impediment to vertical movement of the isotope in solution. The problem of forest floor heterogeneity was addressed above and soil solution nutrient concentration appears to be subject to similar variations. Chapin (1980) reviewing the mineral nutrition of wild plants stated that a 2- to 3-fold variation in soil solution concentration within a few centimeters is not uncommon.

This is a somewhat troublesome problem that would certainly make a mathematical treatment of flow and transfer rates very difficult if not impossible. Shipley and Clark (1972) in their treatise on tracer methods for *in vivo* kinetics stated that formulae for non-steady-state systems, such as would have to be employed in this case, are very complex. They restricted their treatment of the subject matter to the derivation of formulae for only one pool that receives no reflux from other pools and has constant transfer rates. All assumptions that clearly were not met by the dynamic system under investigation here. To overcome the problem of mixing of the isotope and simulate steady-state conditions it might be necessary to transfer forest floor material to the laboratory and treat it there under conditions of controlled moisture and temperature. Artificial environment can be useful in eliminating or controlling environmental parameters that might otherwise be difficult to understand in the field.

The lack of instantaneous and homogeneous mixing of label with substrate, especially in the case of Bonanza Creek, should not detract from the more descriptive approach to describing nitrogen dynamics in black spruce forest floor, that had been chosen for this discussion.

Selected Parameters of Soil Solution at Washington Creek

Lysimeters have been widely used in agriculture and forestry

for over 250 years (Cole et al. 1961). They have been commonly employed to study leaching losses (Overrein, 1968; 1969), fertilizer movement (Patwary and Raikovich, 1979) and evapotranspiration (Fritschen et al., 1977). Different types of lysimeters and their usefulness and application for various field conditions were recently reviewed by Silkworth and Grigal (1981) and Van der Ploeg and Beese (1977). It is generally agreed that the installation of tension plate lysimeters will result in the least amount of disturbance to the soil profile above (Cole, 1958; Goh et al., 1979). Cochran et al., (1970) and Goh et al, (1979), however, cautioned that estimates of nutrients passing through the plates and volume of leachates collected can be highly variable. Thus, Cochran et al., (1970) measured leachate volumes from plates maintained at a constant tension that varied between 1.9-629.9% of the total water applied through rainfall and/or irrigation. Amounts of K passing through the plates ranged from 0.02-86.1% of that applied at the surface.

For the purpose of this study plates were installed primarily to qualitatively monitor ^{15}N export in the soil solution from the forest floor to deeper layers and to further evaluate the filtering capacity of the moss layer with regard to N movement. Quantification of water movement per se was considered of secondary importance. Table 11 shows daily water movement rates through the forest floor at Washington Creek. Volumes collected from the two plates on the $^{15}NH_4Cl$ treated plot showed closer agreement than from the

plates on the $K^{15}NO_3$ treated plot. The reason for the observed variability in daily flux rates can be attributed to differences in forest floor moisture rentention and flow properties of the layers in combination with the irregularity of layer thickness at the two locations within the individual plots. If there was lateral flow to plate surfaces daily flow rates may have been over-estimated (Cochran et al., 1970).

Percent N, C, and C/N ratios for the soil solution collected is shown in Table 12. Percent N in the soil solution was invariably higher and %C lower than the forest floor components it passed through (cf. Table 4), resulting in generally lower C/N ratios of the material analysed. This would indicate conditions somewhat more conducive to decompositon and release of organically bound N (Nommik and Popovic, 1971; Van Cleve, 1974) compared to the forest floor proper. On the other hand, C/N ratios of 30-50 are probably still high enough for microbes to be effective competitors in N retention in the soil solution. Release of N into this medium from the forest floor layers, must be extremely slow as enrichment levels of soil solution N were low on the $^{15}NH_4Cl$ treated plot. Since vascular understory plants and their roots were also poorly tagged plant uptake cannot be the major responsible pathway by which N is pulled out of the nutrient cycling scheme. Nitrogen immobilization and storage (including retention of the positively charged NH_4-N ion) in forest floor layers, including the mosses, emerge as the

Table 11. Quantities of soil solution ($l \cdot m^{-2} \cdot day$) passing through the forest floor on $^{15}NH_4Cl$ and $K^{15}NO_3$ treated plots of the permafrost-dominated site during the summer of 1978.

Date	$^{15}NH_4Cl$ Applic. Plate 1	Plate 2	$K^{15}NO_3$ Applic. Plate 1	Plate 2
7/26	11.53	12.37	8.56	2.56
8/3	8.36	8.01	5.72	1.79
8/16	2.02	2.23	0.27	0.67
8/23	4.94	5.44	2.97	1.15
8/30	5.23	-	1.24	5.36
9/6	3.87	5.86	4.62	1.00
9/19	2.81	3.29	3.25	0.73

major agents acting on nitrogen dynamics in these ecosystems.

On the $K^{15}NO_3$ treated plot nitrogen export below the forest layers was indicated by a pulse in atom % excess ^{15}N in the soil solution on August 3, and a second, smaller one on Sepember 6 (Fig. 27). Both export peaks were preceded by rainfall although frequent and heavy rain during the second half of August did not cause additional removal of ^{15}N. This indicates that the majority of ^{15}N that could be leached on the $K^{15}NO_3$ treated plot was removed early on in the experiment. Low rates of ^{15}N movement in the soil solution were recorded between August 23 and September 6, a period with almost no precipitation. On the $^{15}NH_4Cl$ treated plot atom % excess values of the soil solution were much lower reflecting reduced N export on this treatment compared to the $K^{15}NO_3$ treated plot. This confirms the earlier contention that the negatively charged NO_3-N ion is subject to leaching losses below the 021+022 layer, the major rooting zone in these two black spruce stands.

Table 13 shows daily total N, C, and ^{15}N movements through the forest floor in soil solution. Expressed this way it can be shown that tagged N moving with the soil solution represents only a small fraction of the total N. The 0.0591 and 0.0759 mg of ^{15}N collected from plate 1 and plate 2 on the $^{15}NH_4Cl$ treated plot represented only 0.02 and 0.04%, respectively of total N that moved through the forest floor profile during the experimental period. Quantities of ^{15}N from

Table 12. Percent total N, %C and C/N ratios of the soil solution on $^{15}NH_4Cl$ and $K^{15}NO_3$ treated plots of the permafrost-dominated site during the summer of 1978

	Date	$^{15}NH_4Cl$ Plate 1	$^{15}NH_4Cl$ Plate 2	$K^{15}NO_3$ Plate 1	$K^{15}NO_3$ Plate 2
	7/26	1.05	0.97	0.88	0.69
	8/3	0.75	0.69	0.64	0.63
	8/16	1.31	-	1.44	-
%N	8/23	0.79	0.76	0.78	0.95
	8/30	1.02	0.68	0.87	0.67
	9/6	0.99	0.54	0.75	-
	9/19	0.72	0.90	0.85	0.72
	7/26	32.97	39.31	31.77	30.68
	8/3	30.54	26.22	32.74	33.55
	8/16	28.99	-	29.16	-
%C	8/23	30.89	28.72	30.95	32.35
	8/30	34.14	29.25	33.29	31.25
	9/6	35.34	30.11	32.30	-
	9/19	34.12	43.36	32.44	31.54
	7/26	31.40	40.53	36.10	44.46
	8/3	40.72	38.00	51.16	53.25
	8/16	22.13	-	20.25	-
C/N	8/23	39.10	37.79	39.68	34.05
	8/30	33.47	43.01	38.26	46.64
	9/6	35.70	55.76	43.07	-
	9/19	47.39	48.18	38.16	43.81

Table 13. Total C, N, and ^{15}N movement ($mg \cdot m^{-2} \cdot day^{-1}$) in soil solution on $^{15}NH_4Cl$ and $K^{15}NO_3$ treated plots of the permafrost-dominated site during the summer of 1978.

		$^{15}NH_4Cl$ Applic.		$K^{15}NO_3$ Applic.	
	Date	Plate 1	Plate 2	Plate 1	Plate 2
	7/26	10.41	11.46	8.52	1.77
	8/3	4.86	5.33	3.94	1.11
	8/16	5.12	-	1.95	-
$N_{Tot.}$	8/23	2.53	2.98	2.56	1.37
	8/30	4.18	-	0.37	4.33
	9/6	1.48	1.79	1.50	-
	9/19	1.68	2.32	2.99	0.44
Total		*247.47	174.95	177.89	65.12
	7/26	328.74	465.27	307.78	78.83
	8/3	197.91	202.68	201.32	59.27
	8/16	113.33	-	39.51	-
$C_{Tot.}$	8/23	99.04	112.73	101.70	46.78
	8/30	139.97	-	14.02	202.11
	9/6	52.76	99.85	64.71	-
	9/19	79.66	111.72	114.09	19.39
Total		*8106.98	9511.92	5382.05	3764.14
	7/26	0.0010	0.0034	0.0009	0.0023
	8/3	0.0024	0.0005	0.0158	0.0029
	8/16	0.0015	-	0.0018	-
^{15}N**	8/23	0.0015	0.0003	0.0015	0.0004
Tot.	8/30	0.0000	-	0.0000	0.0004
	9/6	0.0000	0.0013	0.0021	-
	9/19	0.0003	0.0021	0.0000	0.0002
Total		0.0591	0.0759	0.1966	0.0841

*mg/m^2 for the duration of the experiment

**Isotope applied at a rate of 310.40 and 101.81 $mg \cdot m^{-2}$ on $^{15}NH_4Cl$ and $K^{15}NO_3$ plots, respectively (cf. Table 3)

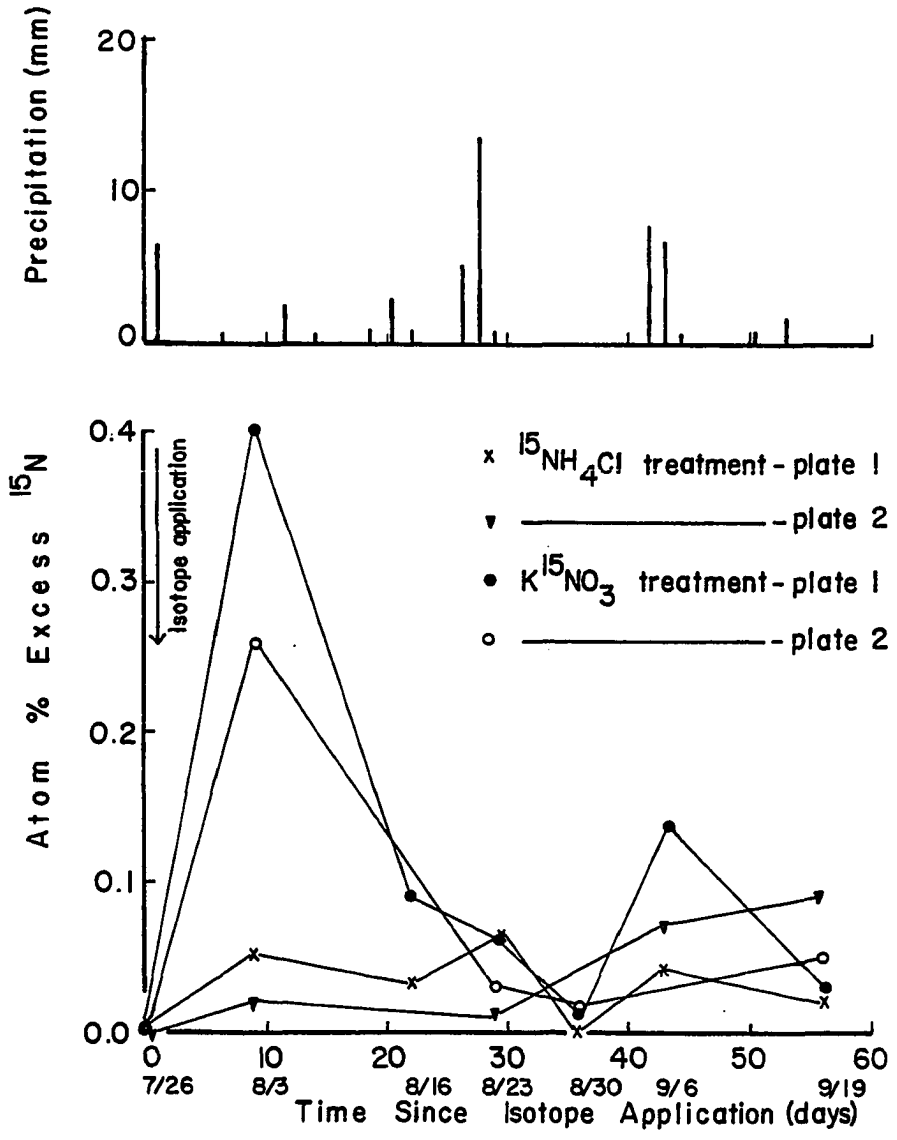

Figure 27. Atom percent excess ^{15}N in the soil solution of $^{15}NH_4Cl$ and $K^{15}NO_3$ treated plots at Washington Creek in 1978 and precipitation data for that summer

the $K^{15}NO_3$ treated plot were larger, as could be expected, but still only made up 0.11 and 0.13% of total N collected from plate 1 and plate 2, respectively. These percentage values are also fairly representative of the amount of ^{15}N that moved through the respective treatment plots when calculated on the basis of the original isotope application. Specifically, of the 310.40 mg $^{15}NH_4Cl \cdot m^{-2}$ applied 0.02 and 0.02% were recovered from plate 1 and plate 2, respectively. On the $K^{15}NO_3$ treated plot of the 101.81 $mg \cdot m^{-2}$ applied 0.19 and 0.09% moved through plate 1 and plate 2, respectively, further illustrating the filtering activity provided by the forest floor to any movement of N out of the system by leaching.

In comparison, the amount of carbonaceous material collected in the soil solution was fairly large. It is presently unknown what these values mean in terms of potential energy sources for the microbial populations in the forest floor.

Examination of the soil solution thus revealed slow nitrogen export from the system via this pathway and served as a check on the earlier contention that nitrogen is effectively retained and cycled within the forest floor layers.

CONCLUSIONS AND RECOMMENDATIONS

The cold-dominated nature of the northern boreal forest places constraints on ecosystem structure and function that are either unique to these systems or more strongly developed than in more temperate ecosystems. Soil temperatures are low, favoring the formation of permafrost and slow forest floor decomposition rates. The use of ^{15}N as a tracer for nitrogen dynamics in the forest floor has proven to be a useful tool for understanding some of the controls that operate in high latitude black spruce forests. Application strength at 100% of the available forest floor nitrogen pool sizes proved best for monitoring nitrogen dynamics, at least for up to three years, after introduction of the tracer into the system. With sufficiently large natural pool sizes, however, as was the case on the $^{15}NH_4Cl$ treatment at Bonanza Creek, isotope application at only 10% of the available pool size was adequate to monitor N dynamics for the duration of the experiment.

A thick carpet of mosses, made up primarily of the feather moss species Hylocomium splendens and Pleurozium schreberi, seemed to play a vital role in the nitrogen economy of the forest floor and hence the black spruce stand as a whole. Nitrogen intercepted by the mosses from atmospheric deposition (precipitation, leafwash, dust), or fixed by epiphytically growing blue-green algae, would be quickly immobilized in the green and, to a lesser extent, in the brown

moss compartment and retained there in order to be released very slowly to the lower organic layers of the forest floor where most of the vascular plant roots are located. Vascular understory plant ^{15}N uptake was minimal and so was ^{15}N export via the soil solution. The long-term storage compartment of ^{15}N on a unit weight basis was the moss component, but the 021+022 layer, by virtue of its large mass, contained most of the ^{15}N on a unit area basis. The isotopic tracer technique, thus, provided the opportunity to test one of the contemporary theories of ecosystem strategy, namely that systems will conserve potentially limiting resources, such as nitrogen, by concentrating them and/or withholding them from dilution and loss. Results obtained here, through labelling of the forest floor in conjunction with tension lysimeter installation to collect the soil solution, were consistent with the theory.

Periodic mineralization episodes in the forest floor layers appeared to have been largely restricted to the moss layers since available N pools in the deeper forest floor layers incorporated little label over the three year experimental period. Mineralization/immobilization events seemed to have been more frequent and dynamic at the permafrost-free site at Bonanza Creek than on the permafrost-dominated site at Washington Creek, suggesting more favorable conditions for nitrogen transformations, such as improved organic matter quality (reduced $^{C}/N$ ratio), on the warmer site.

The usefulness of the ^{15}N data in describing nitrogen dynamics was enhanced by using them with reference to other data (Hauck and

Bremner, 1976) such as C/N ratios as an indicator of organic matter quality, seasonal forest floor temperature and precipitation patterns. The working hypothesis, namely that environmental factors control nitrogen transformations, proved to be a helpful framework within which a better understanding could be gained of system functioning in this black spruce ecosystem compartment. The reduced oscillation amplitude in nitrogen pool sizes with depth from the green moss layer on both spruce sites reflected more stable temperature and moisture regimes at increasing depth from the green moss surface and, by implication, emphasized the controlling influence of temperature and moisture over N dynamics in the green moss layer. The 021+022 layer, characterized by lower C/N ratios than the overlying brown moss layer (01), showed permanently little activity in the NH_4-^{15}N and NO_3-^{15}N pools and no activity (failure to incorporate label) in the SO-N pool on both permafrost-free and permafrost-dominated sites. This would indicate temperature and/or moisture rather than organic matter as the overriding factor controlling N flow in lower layers of the forest floor.

The hypothetico-deductive method, furthermore, helped to define the limits of the experimental approach as it was devised for this study. For example, it was difficult to separate the effect of rainfall events from that of forest floor temperature fluctuations upon seasonal nitrogen dynamics, especially at the moss surface. The pattern was not sufficiently consistent to provide

a predictive capability other than the general observation that seasonally fluctuating forest floor moisture regimes appeared to exert a greater influence over N dynamics than seasonal variations in soil temperature. Controlled environment studies would be required to construct response surfaces relating the effect of temperature and moisture to nitrogen transformation processes.

The original intention to express nitrogen flow in terms of steady state flux rates derived from isotope dilution curves was not fulfilled. Violation of assumptions related to sequestering of nitrogen in the moss layers, uneven penetration of the forest floor by the surface applied tracer and lack of instantaneous and homogeneous mixing of label with substrate could not be anticipated and precluded treatment of the data by tracer kinetic methods.

The dominance of NH_4-N over NO_3-N as the ionic form of nitrogen lent further support to the nutrient conservation theory and also pointed to energy conservation in the system, as espoused by proponents of the theory of inhibition of nitrification by late successional ecosystems. Circumstantial evidence gathered here, such as ^{15}N export on the $K^{15}NO_3$ treated plot at Washington Creek and low enrichment levels of the vascular (whole) plant component, would support this contention; but additional information relating to microbial species composition and allelopathic interactions would be required if one were to accept or reject this scenario

of ecosystem strategy. Furthermore, the problem of small nitrogen pools turning over rapidly vs. large pools turning over slowly should be addressed specifically in future investigations by examining N flux rates rather than static pool sizes. The rapid mobilization of the isotope after introduction into the precursor pools would indicate a rapid flow rate through the available pools (particularly NO_3-N) obviating the need to invoke allelopathic inhibition of nitrification to explain the small NO_3-N pool size.

Another possible avenue for future research could involve a refinement of the technique employed in this study in order to accumulate more knowledge about these extensive ecosystems. It has become clear that low levels of highly enriched isotope are well suited for studying natural systems, but more attention should be given to the inherent natural variability of the forest floor. The problem of heterogeneity can be circumvented by either increased sampling intensity, which may be prohibitive in terms of time and cost involved, or by initiating laboratory experiments in which some of the variables, including temperature, moisture, and forest floor thickness, can either be eliminated or brought under better control of the investigator.

Research into structure and function of interior Alaskan black spruce ecosystems should continue. Not only because this species occupies such a large area of the State, but also because a more thorough understanding has to be achieved as to how information

gathered in one region of its range can be extrapolated to other sites occupied by black spruce. In this way, an information base would be provided that could be used in the decision making process leading to sound management or treatment of these vast areas of North America.

SUMMARY

The following controls were hypothesized to exert influence over ^{15}N dynamics in the forest floor of permafrost-free and permafrost-dominated black spruce ecosystems in interior Alaska: temperature, moisture, and organic matter quality (C/N ratios).

The effect of moisture was difficult to separate from that of temperature upon N dynamics, but their joint controlling influence over N transformations on both sites was demonstrated by more frequent seasonal mineralization/immobilization events in the green and brown moss layers which were subject to greater climatic fluctuations than the deeper forest floor layers (021+022).

Improved organic matter quality (lower C/N ratio) on the permafrost-free site was conducive to the more dynamic nature of N transformations, as indicated by higher seasonal frequency and amplitude of available pool size oscillation compared to the permafrost-dominated site. This finding would be consistent with available information on the two black spruce sites, the permafrost-free site being characterized by higher above ground tree biomass and production and lower forest floor depth than the permafrost-free site.

The feather moss layer acted as a filtering agent, slowing downward movement of the isotope into the 021+022 layer where most of the vascular plant roots were located. Nitrogen export via the soil solution was minimal, as was vascular plant uptake. The forest floor, thus, acted as a nutrient sink conserving a scarce resource.

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